Prosociality, social cognition and empathy in psittacids and corvids

by

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Ich versichere hiermit an Eides statt, dass die vorliegende Dissertation mit dem Titel "Prosociality, social cognition and empathy in psittacids and corvids" von mir selbstständig und ohne unerlaubte Hilfe angefertigt ist.

München, den 06.11.2017 Agatha Liévin-Bazin

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Hiermit erkläre ich, dass die Dissertation nicht ganz oder in wesentlichen Teilen einer anderen Prüfungskommission vorgelegt worden ist und dass ich mich nicht anderweitig einer Doktorprüfung ohne Erfolg unterzogen habe.

München, den 06.11.2017 Agatha Liévin-Bazin

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Prosociality, social cognition and empathy in psittacids and corvids

Under the supervision of

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Foreword

This PhD project has been carried out in co-supervision between a French university (Université Paris Nanterre, France) and a German university (Ludwig Maximilians Universität Munchen, Germany).

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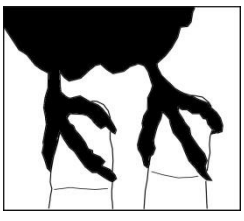

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Si tu peux voir détruit l'ouvrage de ta vie
Et sans dire un seul mot te mettre à rebâtir,
Ou perdre en un seul coup le gain de cent parties
Sans un geste et sans un soupir ;

Si tu peux être amant sans être fou d'amour,
Si tu peux être fort sans cesser d'être tendre,
Et, te sentant haï, sans haïr à ton tour,
Pourtant lutter et te défendre ;

Si tu peux supporter d'entendre tes paroles
Travesties par des gueux pour exciter des sots,
Et d'entendre mentir sur toi leurs bouches folles
Sans mentir toi-même d'un mot ;

Si tu peux rester digne en étant populaire,
Si tu peux rester peuple en conseillant les rois,
Et si tu peux aimer tous tes amis en frère,
Sans qu'aucun d'eux soit tout pour toi ;

Si tu sais méditer, observer et connaitre,
Sans jamais devenir sceptique ou destructeur,
Rêver, mais sans laisser ton rêve être ton maitre,
Penser sans n'être qu'un penseur ;

Si tu peux être dur sans jamais être en rage,
Si tu peux être brave et jamais imprudent,
Si tu sais être bon, si tu sais être sage,
Sans être moral ni pédant ;

Si tu peux rencontrer Triomphe après Défaite
Et recevoir ces deux menteurs d'un même front,
Si tu peux conserver ton courage et ta tête
Quand tous les autres les perdront,

Alors les Rois, les Dieux, la Chance et la Victoire
Seront à tout jamais tes esclaves soumis,
Et, ce qui vaut mieux que les Rois et la Gloire
Tu seras un homme, mon fils.

Rudyard Kipling, *If*, 1910, traduit par André Maurois (1918)

La renonciation n'est pas plus permise que la désertion, seule la persévérance mène au succès. Henri-Frédéric Amiel

List of original manuscripts

Four manuscripts have been written from this PhD work and are either submitted or under revision in different scientific journals.

Manuscript 1

Agatha Liévin-Bazin, Dalila Bovet, Maxime Pineaux, Mathilde le Covec, Manfred Gahr, Auguste von Bayern. "Food sharing and affiliation: an experimental and longitudinal study in cockatiels (*Nymphicus hollandicus*)" Submitted to *Ethology*.

Manuscript 2

Agatha Liévin-Bazin, Franck Péron, Lauriane Rat-Fisher, Agathe Colléony, Laurent Nagle, Dalila Bovet. "Are parrots acting prosocially in an experimental task? A case study". Submitted to *Behavioral processes* (under revision).

Manuscript 3

Agatha Liévin-Bazin, Maxime Pineaux, Olivier Clerc, Manfred Gahr, Auguste von Bayern, Dalila Bovet. "Emotional responses to conspecific distress calls are modulated by affiliation in cockatiels (*Nymphicus hollandicus*)". Submitted to *PlosOne* (under revision)

Manuscript 4

Agatha Liévin-Bazin, Maxime Pineaux, Lucie Daubord, Morgan Rohée, Manfred Gahr, Dalila Bovet, Auguste von Bayern. "Effects of social contexts on novel object exploration in neophobic jackdaws (*Coloeus monedula*)". Submitted to *Behaviour*

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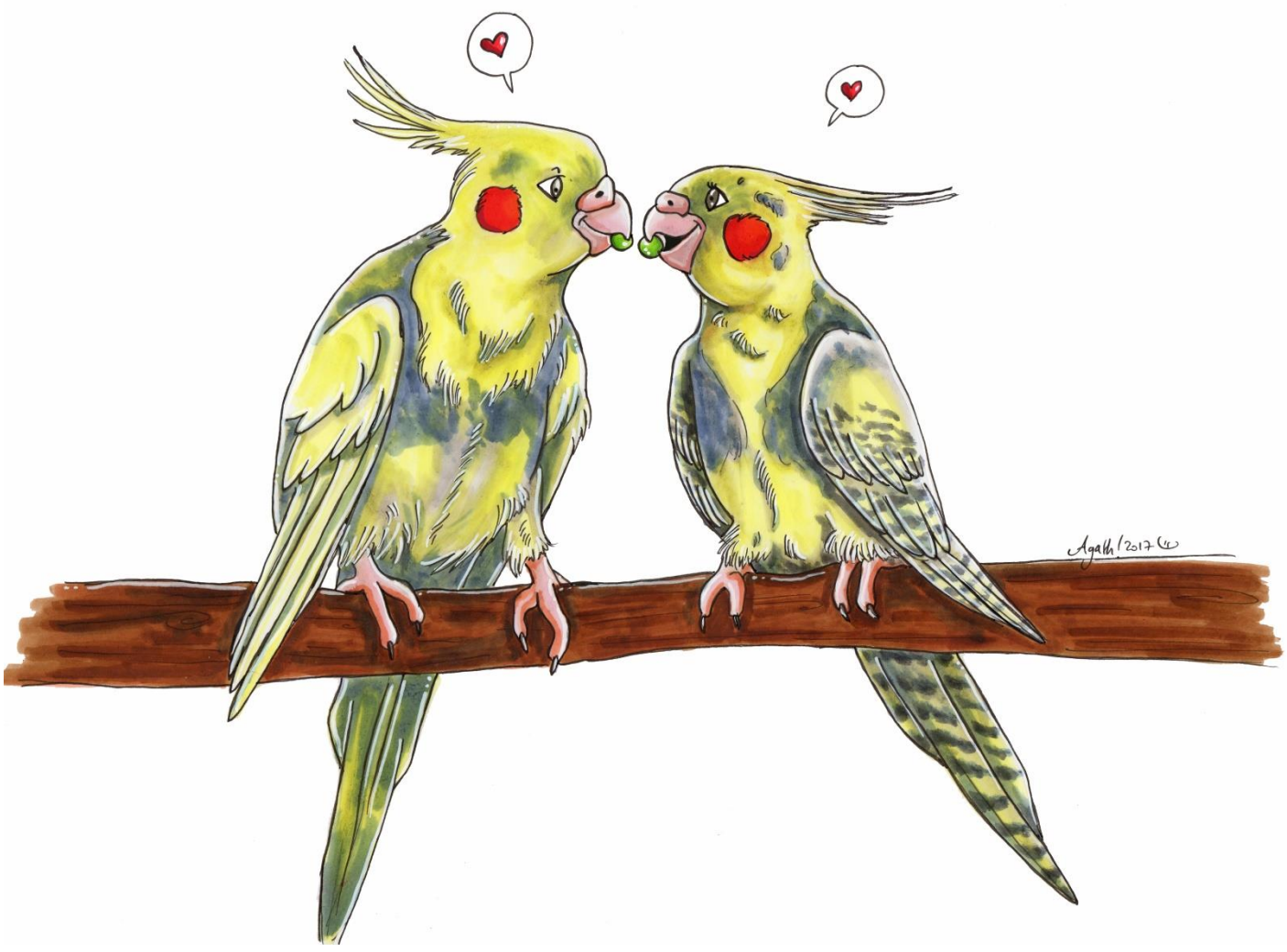
Introduction



Introduction

Since the foundation of ethology as a scientific field, researchers have been fascinated by the emergence of intelligence across animal taxa. Intelligence can be defined and measured "by the speed and success of how animals, including humans *Homo sapiens*, solve problems to survive in their natural and social environments" (Roth & Dicke, 2005). It is still difficult to characterize intelligence precisely among all different species due to radical differences in animals' ecology but it implies behavioral flexibility, which means that the animal can adapt itself to new constraints, including problems to solve or changes in its environment. Some researchers even defend the existence of emotional intelligence, which suggest that emotion-related and empathic abilities are seen as a particular type of intellectual ability that should overlap with cognitive abilities to some extent (Martin-Raugh et al., 2016). These adaptations are resulting in a high survival rate and fitness of individuals (Humphrey, 1976). Some of the animals classified as the most clever ones are able to perform well in very specific and rare tasks implying the use of Theory of mind, i.e the ability to infer mental states to others such as intention and knowledge (Premack & Woodruff, 1978; Call & Tomasello, 2008), social learning (Templeton, Kamil, & Balda, 1999), tool-use (Matsuzawa, 2008) or even cultural transmission (Whiten & van Schaik, 2007). Most of these sophisticated behaviors appear within complex social groups and the presence of other conspecifics in close proximity may play an important role in the emergence of flexible strategies. Animals have to cooperate, to act prosocial or to avoid competition to maintain good relationships with their partners. Consequently, it is crucial for them to develop strategies directed to others and to pay attention to others' actions, intentions and/or emotional states. Recent evidences revealed that social partners and the degree of affiliation shared between individuals play an important role in the social group structures and may be a predictor of intelligence. However, the question still remains: what are the selective pressures at the origin of animal intelligence? Why do

some species seem to outperform others? And are emotions and affiliation between partners involved in these processes?

I) The emergence of intelligence: sociality wins

Most of the first studies on animal intelligence focused on non-human primates, because studying the complex organizations and behaviors of these animals gives us fascinating and meaningful insights of the emergence of intelligence in our own species. Moreover, primates are also characterized by unusually large brain for their body size. Many studies focused on the analysis of a precise part of the primate brain to measure intelligence: the neocortex. It is usually considered as being involved in cognitive processes associated with reasoning and consciousness (Dunbar, 1998). Most of the literature used the relative neocortex size (i.e relative to overall brain size) as the main variable and predictor of intelligence in primates (Dunbar, 2009). Of course, brain sizes scale allometrically with body size (Jerison, 1970) but some animals exhibit larger brains that predicted. And since having a big brain costs a lot of energy to produce and maintain, it is very likely that these big brains are adaptations (West, 2014).

1) Ecological hypothesis of the emergence of intelligence

Several hypothesis were proposed to explain the emergence of intelligence and consequently the increase in brain size in primates (Dunbar, 1992), and in other animal taxa such as rodents (Mace, Harvey, & Clutton-Brock, 1981), bats (Eisenberg & Wilson, 1978), carnivores (Dunbar & Bever, 1998), ungulates (Shultz & Dunbar, 2006). Firstly, several ecological hypotheses suggested that diet, the activity timing and the way animals obtain food could influence the neocortex size. Indeed, some primate species need to adapt their foraging strategies depending on if they eat leaves or seasonal fruits, which are ephemeral resources

that need to be geographically localized and memorized. Several studies showed that frugivorous primates displayed a relative bigger brain compared to their body size than folivores (Clutton-Brock & Harvey, 1980; Milton, 1988). A more recent study which investigated more than 140 primate species even argued that only diet could be relevant to explain the increase in brain size (DeCasien, Williams, & Higham, 2017). In bats, the frugivorous species exhibit the biggest relative brain size compared to insectivores (Eisenberg & Wilson, 1978). Another ecological hypothesis called the "extractive foraging" hypothesis postulated that brain size would increase if the individual need to use special techniques or tools to obtain a food, like for example cracking a nut open or to use stick to fish for termites (Van Lawick-Goodall, 1966). Besides, hunting could also imply brain power, especially in cooperative cases where strategies and synchrony are observed in individuals (Boesch, 1994). Indeed, a predator, which needs to hunt and take into account its potential preys' reactions, would not need the same cognitive abilities as herbivores (Gibson, 1986). Another alternative ecological explanation for the emergence of intelligence was the activity timing. The fact to be diurnal or nocturnal could have an influence over the development of the brain size and the cognitive abilities. In small mammals including soricidae (shrews), sciuridae (squirrels) and bathyergidae (mole rats), relative neocortex size is larger in nocturnal than in diurnal lineages (Mace et al., 1981). In primates, studies described contrasting results: neocortex has been found larger in diurnal primates than nocturnal primates (Barton, 1996) whereas no significant differences has been found in another previous study (Clutton-Brock & Harvey, 1980). However, it seems that a large portion of the primate neocortex is involved in visual processing, and not in true cognitive functions. Even if a continuity exists between visual and cognitive processing, results should be analyzed cautiously and a clear distinction between sensory specializations would be hard to investigate (Barton, 1996; Joffe & Dunbar, 1997).

2) The Social Intelligence Hypothesis

One of the first popular explanation of the increase of brain size and complex cognition in primates resulted from the complexity of social organization: the Social Intelligence Hypothesis (SIH). One of the first studies ever published investigated lemurs and other monkeys social troops and highlighted the fact that "some social life preceded and determined the nature of primate intelligence" (Jolly, 1966). Another study argued that ecological constraints could not be powerful enough to explain the superior abilities of primates over other species, whereas sociality would be (Humphrey, 1976). And some skills like tool-use to obtain food (illustrating the extractive foraging hypothesis) are most of the time acquired by mimicking others, suggesting that the social environment plays an important role anyhow. Twenty years later, another famous hypothesis integrated in the SIH, emerged and tried to define more precisely the impact of sociality on primates' intelligence: the Machiavellian Intelligence Hypothesis (MIH) (Byrne & Whiten, 1988). Even if living in groups present advantages such as reducing the predation risk due to an increase of vigilance by the different members of the troop, it also represents high costs like resources competition. The Machiavellian Intelligence Hypothesis is inspired by the principles detailed by Niccolo Machiavelli in his book *The Prince* published in 1513: politicians need to lie, to be dishonest and to socially manipulate others for their own profit (Byrne & Bates, 2007). The MIH postulates that the brain of primates increased in size because of competition and tactics used by animals to maximize their own success such as deception, manipulation, alliance formation, exploitation of the expertise of others to steal food, etc. This success over others is transformed into reproductive success selecting for larger and more complex brains (Gavrilets & Vose, 2006).

a) Neocortex size correlates with group size in primates

The first quantitative evidences validating the Social Intelligence Hypothesis (SIH) were materialized by a positive correlation between the relative neocortex size and the size of social groups in primates (Dunbar, 1992). Strikingly, neocortex size did not correlate with any index of the ecological hypotheses but did with social group size (Dunbar, 1998). On the other hand, some studies proposed other explanations than sociality to explain this increase of brain size like diet in primates (DeCasien et al., 2017) or the development of areas dedicated in perception and provoking brain size increase (Barton, 1996). Nevertheless, these explanations only worked with relative brain size and not with the measure of neocortex. However, it is likely that neocortex has been the subject of different type of selection pressures, both ecological and social (Dunbar & Shultz, 2007a). Even if these results are highly debated, the SIH is still very popular and represents a very satisfying explanatory possibility of the emergence of intelligence.

b) Social intelligence is not uniquely found in primates

After focusing on our closest relatives for years, researchers found that the exact same correlation between the relative neocortex size and the mean size of social groups exists in other taxa too. Indeed, several other species exhibit complex societies coupled with cooperative actions or high rate of problem solving (Benson-Amram, Dantzer, Stricker, Swanson, & Holekamp, 2016). First investigations focused on mammals and showed a correlation between group size and neocortex ratio in carnivores and insectivores such as mustelids, ursids, canids and felids (Dunbar & Bever, 1998). The same correlation is observed in cooperative hunters like spotted hyenas *Crocuta crocuta* (Holekamp & Benson-Amram, 2017), dolphins (Marino, 2002; Connor, 2007), bats (Pitnick, Jones, & Wilkinson, 2006) and ungulates (Pérez-Barbería, Shultz, & Dunbar, 2007; Pérez-Barbería & Gordon, 2005) or sciuridae (squirrels) (Mace et al., 1981). Even if the correlation had not been tested, some

evidence suggest that elephants would be good candidates to illustrate the link between neocortex size and sociality since they are long-lived and have a very complex and rich social life (Shoshani, 1988; Shoshani, Kupsky & Marchant, 2006). Some recent findings even described that absolute brain size (not relative brain size) increased with sociality in ground squirrels, exhibiting several levels of sociality (Matějů et al., 2016).

3) A refinement of SIH

a) Social complexity instead of group size as a predictor of brain size

Interestingly, several studies found results matching the brain size to the social complexity, instead of the group size. Indeed, in primates, the relative neocortex size does not only correlate with the social group size (Sawaguchi & Kudo, 1990), but also with other factors suggesting social complexity in primates such as the size of the grooming clique (Kudo & Dunbar, 2001), the rate of social learning and innovation (Reader, 2003), the rate of social play (Montgomery, 2014) or the frequency of tactical deception (Byrne & Corp, 2004). Consequently, a refinement of the SIH examines the complexity rather than the number of relations to handle, favoring the quality over the quantity. Groups being socially complex have been usually defined as those in which individuals form long-term pair bonds and/or maintained long-term reciprocal relationships (Dunbar & Shultz, 2007b).

Multiple species displaying these correlations between brain size and social complexity seem to live in fission-fusion groups. In these dynamic groups, big social group split into smaller subgroups. Subgroups merge again when all animals spend the night in the same place, for example. Being part of a big social group over a long period of time implies to take others into account and to remember past interactions. It is especially the case in these fission-fusion groups, where group composition is dynamic: frequently splitting and merging in smaller subgroups has been proposed as one of the aspects of social complexity (Sueur al., 2011b).

These fission-fusion dynamics have been observed in some of the species described above, whose relatively big brains could be explained by the social brain hypothesis (elephants *Loxodonta africana*, Couzin, 2006; chimpanzees *Pan troglodytes*, Sueur et al., 2011a; Amici, Aureli, & Call, 2008; orangutans *Pongo pygmaeus*, van Schaik, 1999; dolphins *Lagenorhynchus obscurus*, Pearson, 2009; bats, Kerth & Konig, 1999, Willis & Brigham, 2004; corvids, Bugnyar, 2013). Consequently, in these dynamic groups, individuals modify the persistence of associations with certain others, and sometimes smaller social associations emerge like small family groups constituted of parents and their offspring or mated pairs.

In birds, correlation between relative brain size and group size could not been found (Dillard & Westneat, 2016). Moreover, previous investigations failed to show any relationship between relative brain size and social association (cooperative breeders versus non cooperative breeders; Iwaniuk & Arnold, 2004) and propensity to flock in birds (Beauchamp & Fernández-Juricic, 2004). Consequently, it has been proposed that the relative brain size in birds is correlated with the strength of pair-bonds rather than to group size and other sociality index (Shultz & Dunbar, 2010). Indeed, the pair is the more common and stronger social unit in birds (Emery et al., 2007). This assumption has been validated by a recent finding suggesting that brain size correlates with social monogamy (but not genetic monogamy) in birds (West, 2014).

b) Social monogamy at the core of social complexity

Forming exclusive pair-bonds, even if it represents the simplest social aggregation, at the core of social complexity, is a highly cognitive demanding type of association and may be a more robust predictor of brain size than group size (Emery et al., 2007). Social monogamy appears in several species of mammals such like Ethiopan wolves *Canis simensis*, North American beavers *Castor canadensis*, Bornean gibbons *Hylobates muelleri* (Cohas & Allainé, 2009) or

Prairie voles *Microtus ochrogaster* (Williams et al., 1992), but it is considerably more widespread among avian species.

Many birds may form lasting pair-bonds with their partners, and not in stable social groups as it is commonly observed in parrots (Spoon et al., 2007), corvids (Baeyens, 1981; Emery et al., 2007), or geese (Black, 2001). Contrary to primates and other mammals which are rarely sharing an exclusive sexual bond with a preferred partner (Clutton-Brock, 1989; Kleiman, 1977), birds are involved in monogamous relationships 90% of the time (Lack, 1940; Lack, 1968).

The definition of monogamy can be plural and one of the most widely accepted definition is " a prolonged association and essentially exclusive mating relationship between one male and one female" which imply that occasional covert mating outside the pair bond do not negate the existence of monogamy (Wittenberger & Tilson, 1980). Monogamy is also "generally recognized in the field and in captivity by a variety of less stringent characteristics, including (1) the continual close proximity of an adult opposite-sex pair both during and outside periods of reproduction (2) mating preferences, and (3) an absence of adult unrelated conspecifics from the pair's home range, territory or nest, (4) Breeding by only one adult pair in a family group also supports the probability of monogamy" (Kleiman, 1977). In birds, the concept covers both species with long term relationships and species in which the pair bond is only maintained with the female after mating and during the rearing of offspring (Lack, 1968). Previously, Lack (1940) also exposed another older classification of monogamy based on the length of the pairing bond (Heinroth, 1928). He distinguished different groups including partners meeting only for copulation, partners staying together for a few days, for a complete breeding season or for life. The two last categories are the most interesting ones because they imply a real investment in the partner over a long period of time and the emergence of a rich social life.

Even if most birds are described as monogamous and form pair-bonds, a clear distinction needs to be made between social and genetic monogamy. In the case of social monogamy, the two partners cooperate to raise offspring and stay together even if some extra pair copulations occurr whereas in genetic monogamy, the mating events only happen inside the mated pair. Contrary to the first studies on monogamy in bird (Lack, 1968), it is now commonly accepted that socially monogamous species have an average frequency of extra pair offspring being 11.1% of offspring and 18.7% of broods. True genetic monogamy with no extra-pair copulations has been found in less than 25% of socially monogamous bird species studied to date (Griffith, Owens, & Thuman, 2002).

The function of social monogamy seems to be centered around exclusive access to a mate but it also appears that it enhances the ability of the mated partners to gain more access to resources for breeding and survival (see Mock & Fujioka, 1990 for review). Moreover, the pair-bond is a perfect illustration of cooperative behaviors (Black, 1996): parents work as a team to construct the nest, to incubate the eggs and to take care of the chicks. Sexual partners in birds cooperate and synchronize behaviors during and sometimes outside the breeding season, in both reproductive and non-reproductive context (Black, 1996): they spend time in proximity even outside breeding season (magpies *Pica pica*; Birkhead, 1979), synchronize their actions (jackdaws *Coloeus monedula*; Röell, 1978), defend the nest conjointly against predators (great tits *Parus major*, Regelmann & Curio, 1986), they form coalitions and assist each other by joining in aggressive encounters and by inhibiting other birds from threatening their mates (Bewick swans *Cygnus coumbianus*; Scott, 1980). Partners also spend an important amount of time at preening each other and it has been demonstrated that preening is not only involved in strengthening social bonds but also in increasing fitness in common guillemots while reducing parasites (Lewis et al., 2007). Mated pairs are involved in object joint manipulation (jackdaws; von Bayern et al., 2007), cofeeding (jackdaws; de Kort et al.,

2006) and sing in duet (tropical boubou *Laniarius major*; Grafe & Bitz, 2004; canary-winged parakeet *Brotogeris versicolurus*; Arrowood, 1988; bar-headed geese *Anser indicus*; Lamprecht et al., 1985). Consequently, social monogamy provides many advantages to both partners even outside the reproductive context.

Long-term monogamy is so demanding that it could be one of the main drivers of complex cognition and brain size increase, especially in birds (Emery, 2006; West, 2014). Indeed, it involves a considerable degree of tolerance towards a single conspecific over a long period of time, a high level of synchrony and cooperation and usually outside the context of mating (Kleiman, 1977).

II) Prosociality: benefiting others

Monogamous birds display a high level of cooperation to build nest, feed their partners during the incubation, and raise nestlings. These other-directed behaviors are prosocial behaviors. As defined by Batson & Powell, 2003, "prosocial behavior covers the broad range of actions intended to benefit one or more people other than oneself, behaviors such as helping, comforting, sharing and cooperation. Prosocial behaviors imply a benefit for the recipient and sometimes a cost for the donor. In this latter case, we would call it "altruism" (Batson, 1991). Prosocial behaviors are not exclusively found between monogamous mated partners but are also often observed between affiliates and familiar individuals in social groups (de Waal, 2008; de Waal & Suchak, 2010).

Interestingly, prosocial behaviors appear in a wide range of taxa and in different contexts: cooperative problem solving (primates, Hirata & Fuwa, 2007; parrots, Péron et al., 2011b; canids, Dale et al., 2016), food-sharing via or without token exchanges (primates, Horner et al., 2011; Claidière et al., 2015; de Waal & Suchak, 2010; jackdaws *Coloeus monedula*, von Bayern et al., 2007, Schwab et al., 2012; ravens *Corvus corax*, Lambert et al., 2017; azured-

winged magpies *Cyanopica cyanus*, Horn et al., 2016 ; rodents, Hernandez-Lallement et al., 2015), reciprocal allogrooming and allopreening (impalas *Aepyceros melampus*, Hart & Hart 1992; barn owls *Tyto alba*, Roulin et al., 2016) and helping and rescue behaviors (rodents, Ben-Ami Bartal et al., 2011, 2014).

1) Why acting prosocial?

Providing assistance has a function and is a result of a particular situation. Nevertheless, as previously said by de Waal (2008) and as it was also suggested by Trivers (2002) it is crucial to distinguish the motivational impulse at the origin of the prosocial behavior from evolutionary considerations that maintained it over time. In the present thesis, I present on one side, some models explaining the maintenance of prosociality and how this behavior was selected because of its consequences on individuals' fitness (ultimate causes). On the other side, I describe the main driver of prosociality as an internal motivational mechanism (proximate causes), which refers to the immediate situation that triggers behavior. Some motivational terms like "selfish" or "unselfish" to characterize altruistic strategies have been misused. One could think that when an individual acts prosocial and that this action has some consequences on its own fitness, the animal is selfishly calculating benefits, which is not plausible. Evolutionary analyses may be kept separated from motivational impulses.

Concerning ultimate causes, the main theories explaining the emergence and maintenance of prosociality over time are: kin-selection, mate provisioning, reciprocity, status enhancement and avoidance of aggression. These explanations are not exclusive from each other and, for example, reciprocity can occur between both kin and non-kin individuals.

On the other hand, proximal causes driving prosociality, many options remain. Batson & Shaw explained that the altruistic motivations at the origin of prosociality in humans are mostly self-directed: while helping others, the actor will receive material rewards, public

praise and a good reputation (Batson & Shaw, 1991). Even in the absence of an obvious reward, acting prosocial could be a way to avoid the distress felt while seeing another person in need. Helping the other would be actually done for the ultimate goal of relieving its own distress. It could be also used to feel good about oneself, while helping others. One of the most popular explanation for prosociality in humans is empathy. Following the empathy-altruism hypothesis, and as written by Batson & Shaw (1991) "empathic emotion evokes truly altruistic motivation, motivation with an ultimate goal of benefiting not the self but the person for whom empathy is felt", and it is suggested that empathy and other-directed behaviors may exist in other animals too (de Waal, 2008; Decety et al., 2016).

Consequently, empathy would be the main proximal motivation for prosociality, which would have as an ultimate goal to improve the subject's fitness via mechanisms such as kin-selection, reciprocity, or status enhancement.

2) Ultimate explanations for prosociality

a) Kin selection

Prosociality between closely related individuals, such as parents and offspring or between siblings, can be easily explained by kin selection (Hamilton, 1964). While helping kin, individuals promote the survival and the transmission of their own genes. For example, in primates, the large majority of food-sharing exchanges occur between a mother and her offspring (Silk, 1978, Jaeggi & Schaik, 2011, Jaeggi et al., 2008). Another study in the wild with chimpanzees described that 86% of the instances of banana distribution observed occurred between mother-offspring but also between sibling, uncle-nephew and grandmother-grandchild (Feistner & McGrew, 1989). Cooperative hunting and the sharing of the prey mainly happen in social carnivores groups constituted of family members like in killer-whales *Orcinus orca* (Guinet et al., 2000) or lions *Panthera leo* (Grinnell et al., 1995). The

communal care of the young in cooperative-breeders such as birds (Cockburn, 1998), primates (Cronin et al., 2009) and social mammals like lions, banded-mangooses *Mugos mungo* and meerkats *Suricata suricatta* (see Clutton-Brock, 2006 for review) is another example of prosociality mediated by kin selection. The classical view of cooperative breeding suggests that some individuals stay at their parents' nest, delay their dispersal and help raising their younger siblings. Consequently they maximize the dispersion of their own genes since they share genetic proximity with their siblings (Bergmüller et al., 2007). However, even if young birds may have indirect fitness benefits or delayed benefits while gaining experience to improve their own reproductive success, they do not breed independently and competition may emerge between relatives, which represent a cost (Hatchwell, 2009). Also, some recent studies revealed that helpers are less related to the breeders than has been previously thought. In these cases, the direct benefits of this cooperative behavior have been underestimated since benefits would be strong enough to maintain helping even between unrelated individuals Helpers can indeed increase their direct fitness by raising their survival while staying in large groups, they can also improve their mating success and their ability to rear offspring while being trained at rearing the nestlings of other birds (Clutton-Brock, 2002).

b) Mate-provisioning

Being prosocial can also help to find a mate and improve its own fitness. A recent study in humans investigated the relationships between the willingness to donate the winning of $100 CAD to charity (used as a behavioural measure of altruism) and their mating success (having more sexual partners and more sexual intercourses within relationships). Results showed that altruists have higher mating success than non-altruists (Arnocky et al., 2017). Another study, still conducted in humans, showed that men contributed more to charity when observed by a female, than by a male or when non observed, whereas female charity donations did not vary across the three conditions, suggesting that men's generosity might have evolved as a costly

mating signal (Iredale et al., 2008). In numerous species of insects (Vahed, 1998), birds (Lack, 1940a) and mammals (Kuroda, 1984) males act prosocially to find a partner and offer food to females either before, during or after copulation (Stevens & Gilby, 2004). Consequently, the exchange of food could serve mate attraction and a positive correlation has been observed between courtship feedings and copulation rates in birds, like in common terns (González-Solís, Sokolov, & Becker, 2001). In corvids, some studies suggested that food-sharing between individuals during the juvenile period could be used as a signal to choose a reliable partner (von Bayern et al., 2007; Clayton & Emery, 2007).

c) Reciprocity

One of the most important evolutionary explanations for food sharing, especially between non kin, is reciprocity. Acting prosocially in this case would be influenced on expected future reward or support, which may be assessed from past interactions. We can distinguish direct reciprocity, where subject A helps subject B because B has helped A before from indirect reciprocity, where A helps B because B has helped C before. To observe the emergence of direct reciprocity, an animal should potentially be able to remember past interactions, and the individuals with which he interacted to make the decision to act prosocially. Whereas indirect reciprocity is based on reputation: an individual will choose to help or not depending on past prosocial actions of the partner. Both direct and indirect reciprocity may require developped cognitive abilities (Rutte & Taborsky, 2007). Indirect and strong reciprocity have been found only in humans so far. Less cognitively demanding reciprocity also exists and no recognition of cooperative partners is required. In this case, an individual will help if he previously received help from anonymous partners. This mechanism is called generalized reciprocity and requires no specific knowledge about the partner. Only the previous social experience would influence the propensity to help others. Generalized reciprocity could be at the origin of cooperation among unfamiliar nonrelatives (Rutte & Taborsky, 2007)

Reciprocity represents a high cost, especially when the benefits are delayed. The most iconic example of high-cost reciprocity in which the survival of both individuals is involved, is the food-sharing of blood by vampire bats (Wilkinson, 1984). Vampire-bats (*Desmodus rotundus*) often regurgitate blood to roost-mates that failed to feed and risk to die of starvation quickly (Wilkinson, 1988). Indeed, these bats cannot survive longer than three days without a blood meal, so giving a blood portion to another individual is extremely costly. Interestingly, it has been shown that the reciprocity of food exchanges was the best predictor of food given across the dyad, more than relatedness between individuals or harassment, since the donors initiated more the exchange than receivers (Carter & Wilkinson, 2013). In this particular situation, the donor will be rewarded for its costly gift because the initial receiver will return the favor later, which is in line with the reciprocal altruism hypothesis (Carter & Wilkinson, 2013).

Low-cost reciprocity can also occur when animals exchange goods: food for food, or food for other social trading currencies such as grooming/allopreening (de Waal, 1997a, 1997b; Carter & Wilkinson, 2015) or support in conflict situations, while forming alliances (Seyfarth & Cheney, 1984), which is common in primates. For example, a correlation was observed between grooming and agonistic support in long-tailed macaques (*Macaca fascicularis*): support was related to previous grooming (Hemelrijk, 1994).

However, examples of reciprocity are scarce in non-human animals since longitudinal observations are needed to record and keep tracks of the chronology of interactions between members of the group. Moreover, it is difficult to compare benefits when the exchanged currencies are different (Brosnan & Waal, 2002) .

d) Status-enhancement

Since being prosocial may be costly, like in charity giving, cooperative actions or food-sharing events, it has been argued via the prestige hypothesis that prosociality, and more specifically helping behaviors may be used as a signal which would give information about an

animal's social status. Being more generous, even if it is costly, may enhance that individual's reputation and status in the group and provide benefits, like finding a mate and/or a cooperative partner (Zahavi, 1995). Another study in cooperative-breeder birds, the Arabian babblers (*Turdoides squamiceps*) revealed that high-ranking individuals allofed low-ranking individuals and this exchange was almost always unidirectional. Consequently, the costly signal of food-sharing would be seen as a display of dominance (Kalishov et al., 2005).

Another classical model of giving defined as a means of signaling income in humans is blood donation. Many explanations have been proposed to explain this costly altruistic behavior directed towards unrelated, and even, unknown others. Some argued that it could be driven by the satisfaction that comes from the act of giving (called the "warm glow" effect), or it could also be done to increase the "prestige" of the donor (Harbaugh, 1998). In that latter case, giving may be perceived positively by others, and the donor would benefit if their donations are made public. It has been even argued that monetary reward for donating blood might crowd out the supply of blood donors, because, while receiving a monetary compensation, donors would lose the social esteem associated with the donation (Titmuss, 1970). An experimental study tried to test empirically this theory and proposed to assess the number of subjects accepting to become blood donors while receiving a money compensation or doing it for free. Results showed that more subjects agreed to become blood donors without any payment than when receiving money, and there was a significant effect of crowding out in women: female blood donors dropped from 52% to 30% when the compensation was introduced (Mellström & Johannesson, 2008).

e) Avoidance of aggression

A very different explanation puts forward that donors may act prosocially in order to avoid conflicts and aggressive social manipulation. Some individuals may share food to stop beggars from harassing them (Gilby, 2006). A study in chimpanzees and squirrels monkey

(*Saimiri boliviensis*) investigated the effects of harassment on food-sharing. Food divisibility permitted to control the ability of the owner to defend the food and the beggar's ability to harass. Results demonstrated that when harassment by beggars increased due to the absence of partition, food-sharing by owners increased too in both species, suggesting that donors share to avoid the cost of being harassed (Stevens, 2004).

Animals can also cooperate because there is a cost when they refuse to participate. They can be punished when they deceive partners, be forced to cooperate or just lose benefits while avoiding acting prosocially. A cooperative hunting study in Taï chimpanzees showed that bystanders and latecomers have access to less meat when they do not hunt, when compared to hunters (Boesch, 1994).

Another study in birds demonstrated that dominants can force subordinated to cooperate. The experiment tested keas (*Nestor notabilis)* which had to cooperate in an instrumental task to obtain a reward and only one of the two cooperating birds was rewarded. Dominants birds obtained the rewards most of the time and they even aggressively manipulated their respective subordinate partner to cooperate (Tebbich et al., 1996). However, this latter experimental design did not give equal rewards to partners and may have triggered the aggressive tendencies of dominant birds.

3) Empathy as the main driver of prosociality

There is no doubt that in human beings, empathy plays an important role in other-directed behaviors (Eisenberg & Miller, 1987; Decety et al., 2016) and is the most widely assumed motivation for altruism and prosociality (Batson, 1991). Even if a growing interest have arisen for this question these last twenty years (de Waal, 2008; Panksepp, 2004; Panksepp & Panksepp, 2013), the existence of empathy in animals is still intensively discussed (Vasconcelos et al., 2012).

However, de Waal argued that some behaviors observed in animals, are so costly than no other motivation than empathy could be strong enough to elicit them. In his book *The age of empathy*, de Waal describes many anecdotal events usually observed in captive animals, in which animals are in real danger and their partners take all the risks and are paying important costs to save or protect them (de Waal, 2010). He quoted Jane Goodall's observations, who reported many incidents involving water in captive chimpanzees (Goodall, 2010). Indeed chimpanzees cannot swim, and in many zoos, apes enclosures are surrounded by water-filled moats. A male chimpanzee jumped in the water to reach an infant who had been dropped by an incompetent mother and he lost his life while trying to save the baby. Another anecdote described an incident which happened to Washoe, the language-trained chimpanzee. Another female was in distress, into the water. Washoe raced across two electric wires that normally contained the apes to reach the victim who was widely trashing about. Washoe then grab the female's arms and pulled her to safety. Of course, these observations are rare, but since artificially creating these dangerous and stressful conditions in controlled conditions are fortunately not permitted, these anecdotal events are unique demonstrations of high-cost prosocial acts. de Waal argued that no explanations in terms of mental calculations (like future reciprocity) work to explain these costly responses to others' distress. Indeed, when a chimpanzee jumps in the water while he cannot swim, reciprocity looks like a shaky prediction, which is not worth taking the risk to lose its life.

Empathy has been defined as the capacity to (i) be affected by and share the emotional state of another (e.g emotional contagion), (ii) assess the reasons for the other's state and/or (iii) identify with the other, adopting his or her perspective. This definition of empathy describes three level of growing complexity (de Waal, 2008).

The lowest level of empathy is called "emotional contagion". It is an automatic-like spreading of emotions from individual to another. Emotional contagion is observed when an individual

yawns while seeing another individual yawning (Palagi et al., 2014), when a flock of birds fly away at the same time because one of them heard a threatening noise (Aubin, 1991) or when a room full of human newborns bursts out crying because one of them started to cry (Hoffman, 1975). There is no proof of any understanding of the other's emotional state but only the evidence of quick dispersion of emotions among individuals.

The second level is "sympathetic concern" and it is a step mixing emotional contagion and the appraisal of the other's situation and attempt to understand the cause of the others emotions. The best example and most documented example of sympathetic concern is consolations, which is defined as reassurance provided by an uninvolved bystander to one of the individuals involved in a previous fight (de Waal & van Roosmalen, 1979). This behavior is easy to spot and observe: a third party goes over to the loser of a fight, which is usually showing distress, and gently puts an arm around his or her shoulders. Consolation has been shown to reduce anxiety in the distressed victim. These observations are numerous, with hundreds of consolation events recorded in chimpanzees (de Waal & Aureli, 1996; Romero, Castellanos, & Waal, 2010; Clay & Waal, 2013). More recently, a study showed that consolation via third-party affiliation can be observed in ravens (Seed et al., 2007; Fraser & Bugnyar, 2010a), prairie voles (Burkett et al., 2016) and wolves *Canis lupus* (Palagi & Cordoni, 2009).

The third and higher level of empathy is called "empathic perspective-taking", which can be summarizing by the expression "putting yourself in other's shoes". The individual must be able to understand the other and adopt its point of view. The most compelling evidence of this high level of empathy is targeted help (de Waal, 1996). In this situation the animal is able to identify the other's needs and intentions, which are high cognitive abilities linked to the Theory of mind (Call & Tomasello, 2008), and can provide a specific help so that its partner can obtain what he desired. As helping others is included in the broad range of prosocial actions, it can be difficult to distinguish the empathic impulse to help from its behavioral

manifestation which is the action to help the partner. Nevertheless, many studies in primates revealed that our closest relatives are willing to help (Yamamoto et al., 2009, 2012; Warneken & Tomasello, 2006a) and are able to identify other's needs and desires (see below) (Hare, Call, & Tomasello, 2001).

Not all altruistic behaviors require empathy, though. For example, when an individual vocally attracts others to discover food, or alerts others to an outside threat, the actor is barely taking others into account, which are usually out of sight or not even close to them. As described by de Waal, "the role of empathy is limited to directed altruism, defined as helping, or comforting, behavior directed at an individual in need, pain or distress" (de Waal & Suchak, 2010).

Most experimental studies investigating empathy involve negative situations like stressful situations and conflicts in which pain, distress or fear are induced. Many experiments investigate emotional contagion, which is the simplest level to test and evaluate empathy. In rodents, both rats (Atsak et al., 2011; Kim, Kim, Covey, & Kim, 2010) and mice (Jeon et al., 2010) expressed increased freezing behaviors when seing a social partner in distress, suggesting the emotional contagion of fear. Another study investigated the behavioral responses of domestic hens (*Gallus gallus domesticus*) with their chicks when exposed to a stressful situation involving air puffs. Behavioral responses of the hens were recorded when animals were either exposed to control condition (with no air puff), with air puff directed to the chicks, to the hen or another control with only the noise of the air puff. Hens responded more intensively to the two conditions with air puffs, but the increase of heart rate and maternal vocalization only occurred when the chicks where exposed to the aversive situation. These responses suggest that adult female birds possess at least some of the essential underpinnings of empathy (Edgar et al., 2012). In graylag geese (*Anser anser*), bystanders who observed a conflict involving either their mated partner or a family member experienced

an increase in heart rate, suggesting an increase of distress in the observer and indicated an empathic response (Wascher et al., 2008b)

Many paradigms may be used to investigate empathy in animals. In the present thesis, I will test emotional contagion, the transmission of emotional states from one individual to another through two specific contexts: the broadcasting of distress calls, and the exploration of novel object in neophobic animals, which automatically provoked fear in the subjects.

a) Testing emotional contagion via distress calls playback

Many experiments investigate emotional contagion, which is the lowest level and less cognitively demanding form of empathy (de Waal, 2008; Preston & de Waal, 2002). The transmission of emotional states from one individual to another may manifest in altered sensory, motor, and physiological states of others (i.e. increase in heart rate, locomotion or cortisol level) (Hatfield et al., 1993). Emotional contagion is closely linked to automatic mimicry, the tendency to imitate and synchronize with the movements of others (Prochazkova & Kret 2017). Most studies have focused on mimicry of facial expressions or on body postures, but there are also emotional processes that involve more subtle reactions and synchronous behaviours such as attuning to others' heart rate or pupil size, or the automatic transmission of crying or yawning (Kret 2015). Some studies report not only that playback of human yawning sounds sufficed to provoke yawning in human receivers, but that it even elicited yawning in dogs (and that regardless of the familiarity of the yawning person) (Silva et al., 2012).

This latter study that described the transmission of yawning via playback suggests that acoustic communication may be a useful medium to investigate emotional contagion. Vocalizations can indeed encode a broad range of information about the emitter such as identity, age, weight (Reby & McComb, 2003), sex, kinship (Rendall et al., 1996) or

dominance status (Mathevon et al., 2010), including emotional states (Perez et al., 2012; Briefer, 2012; Briefer et al., 2015b). Perceiving information about the emitter's emotions can potentially induce the same emotional state in a receiver or may simply increase its emotional arousal (Briefer et al., 2017). Certain types of calls such as alarm or distress calls might have intense emotional salience and may elicit interspecific panic and flight responses in receivers (Aubin & Brémond, 1989).

Distress calls are very specific loud harsh calls emitted when an animal is in a situation of extreme distress such as when sized by a predator or restrained with no possibility to escape (Neudorf & Sealy, 2002) and could be a useful tool to investigate emotional contagion. They are characterized by a complex structure, numerous harmonics, slow modulation in frequency and amplitude and several repetitions (Aubin & Brémond, 1989; Aubin, 1991). In birds, the vocalizations of many species show parallels in acoustic structure and often elicit interspecific responses (Mathevon et al., 1997). In line with this observation, it was found that playback of simplified synthetic calls provoked similar behavioural responses in receivers of different species, e.g in Herring gulls (*Larus argentatus*) and starlings (*Sturnus vulgaris*: the standard response was to approach the sound source first and then flee (Aubin & Brémond, 1989). Another study that tested five different species of birds, reported that the animals responded significantly better to conspecifics distress calls than to those of more distantly related species, however they still reacted to other species' distress calls (Baxter et al., 1999). The exact function of distress calls are still hypothetical and may serve different purposes, e.g. to warn the others of the presence of a predator, to call for help, to distract predators holding prey or to mob enemies (Conover & Perito, 1981; Hill, 1986; Neudorf & Sealy, 2002).

The majority of experiments investigating the reaction of animals to conspecific calls used mammals such as goats *Capra aegagrus hircus* (Briefer et al., 2015b, 2017), horses *Equus ferus caballus* (Lemasson et al., 2009), pigs *Sus scrofa domesticus* (Düpjan et al., 2011), dogs

Canis familiaris (Quervel-Chaumette et al., 2016), rats *Ratus norvegicus* (Saito et al., 2016) or even lizards *Liolaemus chiliensis* (Labra et al., 2016). In birds, most of the studies on distress calls focused on structural (Aubin, 1991), and functional aspects (Neudorf & Sealy, 2002; Conover & Perito, 1981), but did not take into account the social bonds between emitters and receivers. Indeed, studies exploring emotional contagion between conspecifics in birds are scarce. Geese also recruit conspecifics of the flock by emitting calls indicating their mood to fly away. Departure was preceded by an increase in the arousal state of flock members (Ramseyer et al., 2009; Raveling, 1969; Kotrschal, 2012). Most of the studies on birds about emotional contagion that links to familiarity and social interaction focussed on psittacids and corvids, the two avian groups that exhibit the biggest brains relative to body size and the most advanced cognitive abilities (Emery, 2006; Pepperberg, 1990). Budgerigars can "catch" the yawn of others (Miller et al., 2012a, 2012b; Gallup et al., 2015), and birds stretched more in pairing when they could see a conspecific stretching (Gallup et al., 2017), sub-adults ravens synchronize their play (Osvath & Sima, 2014) and keas join into conspecifics' play when they hear specific play calls (Schwing et al., 2017). Parrots are appropriate candidates to investigate responses to conspecifc calls as it has already been demonstrated in several studies that they possess individual vocal signatures (Berg et al., 2011) and are able to recognize others by their voice (Wanker et al., 1998; Buhrman-Deever et al., 2008; Berg et al., 2011; Balsby & Scarl, 2008). Spectacled parrotlets (*Forpus conspicillatus*), for example may use inter-individual variations of six acoustical cues in their contact calls to encode information about the individual (Wanker & Fischer, 2001). These birds are also able to respond differently depending on the emitter of the contact calls, adults preferring to respond to the contact calls of their mates while subadults reacted to the calls of their siblings (Wanker et al., 1998). In the galah (*Eolophus roseicapillus)*, an Australian cockatoo, birds responded differently to the same type of calls, depending on the sex of the

emitter, suggesting that the vocal signal encode informations about the sex and the identity of the emitter (Scarl, 2010). Consequently, investigating birds's behavioural responses to ditress calls could provide valuable insight on the transmission of negative emotions.

b) Testing emotional contagion via neophobia

In nature, individuals are confronted with many dangerous situations throughout their daily life, when foraging, searching for mates or when simply resting. To avoid predators or intoxication by new types of food, animals have evolved strategies to reduce the risks, e.g. related to foraging. One of these strategies is referred to as neophobia, i.e. the aversion of novelty. It is defined as "the avoidance of an object or other aspect of the environment solely because it has never been experienced and is dissimilar from what has been experienced in the individual's past; the concept is associated with fear and the physiological and behavioral correlates of fear responses" (Greenberg & Mettke-hofmann, 2001). In contrast, neophilia is defined as "the spontaneous attraction of an animal to a food item, place or object because it is novel" (Tebbich, Fessl, & Blomqvist, 2009). Avoiding interactions with potential sources of danger can increase the survival of individuals (Ferrari, McCormick, Meekan, & Chivers, 2015) but at the same time represents a cost because it lowers the level of exploration and as a consequence constrains the subject's acquisition of information and discovery of novel resources (Greenberg & Mettke-hofmann, 2001).

Several studies on neophobia in birds have focused on their responses to novel objects (Greggor et al., 2015) and have encompassed a wide range of taxa. Most of these investigated species, particularly the smaller passerines species such as great tits *Parus major* (Dingemanse et al., 2002), zebra finches *Taeniopygia guttata* (Beauchamp, 2000), starlings *Sturnus vulgaris* (Boogert et al., 2006) but also larger passerines such as corvids, e.g. jackdaws *Coloeus monedula* (Katzir, 1982, 1983; Schuett et al., 2012), ravens and carrion

crows *Corvus corone* (Miller et al., 2016), but also galliformes such as japanese quails *Coturnix japonica* (Turro-Vincent et al., 1995) or parrots (Fox & Millam, 2007), all face predation in the wild. Consequently, they all have been found to exhibit high levels of neophobia and escape responses when faced to novel objects.

Many recent studies investigating personality in animals used exploration and neophobia as measurable traits (Réal et al., 2007). Most studies have used the latency to approach a novel object, as the main variable, but because the studies often slightly varied in their methodology, particularly in how the novel stimuli were presented (e.g. whether or not a reward was presented near the novel object, or if the birds were forced to enter novel environments, or whether the novel object/novel food was additionally presented in a novel environment, etc.), the comparability of those variables within and between species studied often remains weak (see Greggor et al., 2015 for review). Moreover a clear distinction need to be made between testing "neophobia", when a novel object is put near food or "neophilia", when novel objects are introduced and experimenter measure the bird tendency to explore these objects out of curiosity (Mettke-Hofmann et al., 2002; Tebbich et al., 2009). Many such studies aimed at characterizing explorative and bold individuals objectively. One of the first hypotheses that arose was that dominance status might play a role in exploratory behavior and neophobia. In zebra finches for example, the level of exploratory activity seems to predict leadership, the tendency to initiate foraging but not high dominance status (Beauchamp, 2000). In a study on jackdaws, "initiators", i.e. the birds that began to feed first on the novel food, were socially mid or low ranking (Katzir, 1983), partly complying with another jackdaw study showing that initiators ranked in the middle of the group's hierarchy (Röell, 1978). In contrast, in ravens (*Corvus corax*), a species of the same genus, social rank did not correlate with approach behavior (Stöwe & Kotrschal, 2007). In domestic dogs (*Canis familiaris*) high ranking individuals tended to manipulate novel objects for longer than low ranking ones but

surprisingly no such difference relating to social rank was found in the closely related wolf (*Canis lupus*), a highly social species in which the social hierarchy plays a predominant role (Moretti et al., 2015). These results suggest that contrary to previous thoughts, less neophobic animals are not necessary high-ranking individuals and exploration and dominance do not seem to be correlated.

Other studies focused on whether the social context may have an effect on subjects exposed to a threatening new object. Most of these studies, tested the subjects in several conditions, i.e. alone, with a preferred partner (usually a sibling), and with a non-preferred partner and/or the entire social group. A comparative study on social groups of dogs and wolves reared under comparable conditions showed that both species investigated the novel object for longer in the pair and in the pack conditions than in the alone condition, suggesting that the presence of other individuals either elicits the exploratory behavior of animals or reduces their neophobia (Moretti et al., 2015). Another study showed that ravens manipulated novel objects more when they were with a partner (dyadic condition) or with the entire group than when they were alone (Stöw et al., 2006b). More recent work on corvids showed that the presence of conspecifics (both that of a single conspecific or that of a group) increased the exploration behavior of both ravens and carrion crows (*Corvus corone*), another corvid species, compared to a condition in which they were alone (Miller et al., 2015). More generally, these different corvid studies found that individuals were very inconsistent in their behavior, both alone and in social contexts (Stöwe et al., 2006a; Stöwe & Kotrschal, 2007; Miller et al., 2016).

Few studies so far have focused on the emotional aspect of neophobia, i.e. the underlying level of stress. The avoidance of novelty is likely to be driven by fear, which often manifests in observable stress-related behaviors. Even if neophobia may be elicited by some sort of automatic escape response which may improve the animal's survival, the possibility of an underlying emotional state ,- fear-, and its transmission from one individual to another

through emotional contagion, the lowest level of empathy (de Waal, 2008) should not be neglected. Neophobia is often expressed via fear- and stress-related behavior induced by a potentially threatening object. Several historic studies investigated the link between fear and social context in animals and demonstrated that the presence of a conspecific effectively reduced the fear response of subjects in rats (Davitz & Mason, 1955), cats (Masserman, 1943) and goats (Liddell, 1950). Other studies on rats also showed that the presence of conspecifics reduced the behavioural signs of fear: male rats exposed to a stressful noise froze less when in a group of conspecifics than when alone. The same study also demonstrated that stress can increase the desire to interact with other individuals: stressed animals sought the presence of a conspecific more than non-stressed animals, suggesting that social contact may alleviate stress to some extent (Taylor, 1981).

The emotional aspect of neophobia was barely tested until now and it appears that the fear associated to novel object exploration could be used to measure the transmission of emotional states from one individual to another. Testing partners sharing a special affiliative bond, could be even more useful to assess the link between emotional contagion and affiliation.

4) The implication of social affiliation in prosociality and empathy

Many factors could influence prosociality, such as the amount of reward obtained by the participants (Range et al., 2009) , the effort of the task (Massen et al., 2012; see Cronin, 2012 for review) or the degree of affiliation and familiarity between individuals (de Waal & Suchak, 2010). In capuchin monkeys (*Cebus apella*), some individuals stopped to participate in an experiment if their partner received a more attractive reward than themselves for equal effort. The effect is even amplified if the partner received a better reward without providing any effort (Brosnan & de Waal, 2003). When a negative reaction to an unequal outcome is observed in the subject, we talk about inequity aversion (IA) (Fehr & Schmidt, 1999).

However, even if IA has an impact on the motivation to act prosocial, affiliation and familiarity also seem to play a crucial role in the maintenance of prosociality (Brosnan, et al., 2005 , 2006; de Waal & Suchak, 2010). Affiliative relationships are commonly described as high quality social bonds between individuals that are usually characterized by the exchange of socio-positive behaviors such as allopreening or allofeeding, as well as by the time spent in close mutual spatial proximity (Simpson, 1973; Nishida, 1972; Mitani et al., 2000). Affiliative relationships can, but must not necessarily be based on genetic relatedness (Mitani et al., 2000). In chimpanzees (*Pan troglodytes*), when given the choice of a cooperative partner, they prefer partners with whom they have a tolerant relationship (Melis et al., 2011) and IA is less pronounced in a group of captive chimpanzees living together for more than 30 years than in a similarly housed group of chimpanzees with a much shorter history (Brosnan & de Waal, 2005). Rats help trapped strangers of a different strain only if they have been previously housed in the same cage with them (Ben-Ami Bartal et al., 2014). In capuchins, prosocial tendencies increase with social closeness (de Waal et al., 2008). The stronger the affinity between two monkeys, the more time they spend together in close proximity and the more they choose the prosocial token to reward their partner (de Waal et al., 2008).

In capuchins, prosocial tendencies increase with social closeness (de Waal et al., 2008). In keas, when tested in a loose-string paradigm where birds had to cooperate to obtain a reward, birds cooperated more with affiliates and were also more successful when tested with affiliates than with non-affiliates (Schwing et al., 2016). The stronger the affinity between two monkeys, the more time they spend together in close proximity and the more they choose to reward their partner (de Waal et al., 2008). Regarding cooperation, familiarity and tolerance enhance it while inequity damage it (de Waal and Suchak 2010; Brosnan & de Waal 2014 for review).

Concerning empathic abilities, they seem to play a role in the formation and maintenance of social bonds (Anderson & Keltner, 2002) and manifestations of empathy such as emotional contagion or consolation are more likely to happen between socially close individuals, sharing strong affiliative bonds. Given that empathy is mostly observed between affiliated or pair-bonded individuals, it is a reasonable hypothesis that emotional contagion is enhanced between such affiliated individuals (Preston & de Waal, 2002;de Waal, 2008). Previous studies have reported that familiarity can play a role in the strength of an emotional reaction to conspecific behaviour, especially in group-living social animals. An experiment in horses showed that they were able to discriminate individuals by their voices, depending on their degree of familiarity. Horses adjusted their behaviour depending on the degree of familiarity they shared with the emitter. Interestingly, horses exhibited the strongest behavioural reactions in response to unfamiliar calls, and lowest in response to group members (Lemasson et al., 2009). A recent study on dogs revealed a heightened stress response in subjects exposed to conspecific whines as opposed to a control sound, but no significant differences were found between their response to familiar whines compared to those of unfamiliar individuals (Quervel-Chaumette et al., 2016). Another study on mice that used a different approach to investigate emotional contagion showed that the animals froze more often when they saw a familiar conspecific receiving electric shocks compared to an unfamiliar individual (Gonzalez-Liencres et al., 2014). Finally, in greylag geese, another study found that the geese increased their heart rates more when they observed affiliated individuals engaged in an agonistic interaction than when they saw fighting non-affiliated individuals (Wascher et al., 2008b).

Indeed, contagious yawning which is a behavior classified as empathic, is more contagious between socially close individuals. In a recent study on yawning in bonobos (*Pan paniscus*) and humans, reported that yawn contagion was higher between individuals sharing affiliative

relationships than between non-affiliated individuals (Palagi et al., 2014). Similar observations have been made in gelada baboons *Theropithecus gelada* (Palagi et al., 2009). Another study on bonobos found that yawn contagion increased when individuals were strongly bonded and when the triggering subject was a female (Demuru & Palagi, 2012). To our knowledge, no study has tested, the impact of affiliative bonds, which should have a much stronger effect than familiarity, in studies on emotional contagion in animals. Similarly to humans, chimpanzees, bonobos and gelada baboons are more likely to yawn when a familiar conspecific yawns, and the closer the social bond between individuals, the more contagious is the yawning. The same results were observed in dogs, linked to the affiliation they share with their owners. The contagious rate of yawning in dogs was higher when the animal saw its owner yawning rather than unfamiliar human models yawning (Romero et al., 2013). In chimpanzees, consolation is provided by kin and other valuable partners, usually the own "friends" of the victim (Kutsukake & Castles, 2004). After a conflict "friends" of the former recipient of aggression offered consolation significantly more often than did friends of the original aggressor and non-friends (Romero & de Waal, 2010). These results are consistent with those observed in ravens (*Corvus corax*), in which consolation from bystander to victim only happens between valuable partners, with which they exchange preening, sit in contact and provide agonistic support.

Concerning neophobia and novel object exploration, affiliation between tested partners also seems to play a role on exploratory tendencies of the subject. Ravens were tested in a paradigm, which exposed the subjects to novel objects or food both alone and in a dyad, which consisted either of siblings or of unrelated subjects. This study distinguished between slow and fast individuals and found that the "fast" birds approached the novel objects quicker when alone, than when tested in dyadic condition. Whereas slow birds' approach was facilitated by the presence of a fast sibling; they explored novel objects quicker and for longer

when paired with fast siblings than when alone (Stöwe & Kotrschal, 2007). A study in Japanese Black and Holstein heifers (*Bos taurus*) recorded the reaction to a novel object in groups of animals. Cows were either in dyads or in group of 5 individuals, which were either familiar or unfamiliar conspecifics respectively. There was a significant effect of familiarity. When exposed to a novel object, cows spent much more time trying to escape when placed in an unfamiliar group than when with familiar conspecifics (Takeda et al. , 2003).

5) Measuring prosociality in artificial conditions

Testing the motivations underlying prosocial actions and the understanding of others' roles are very complex and need experimental studies in laboratories under controlled conditions to precisely assess immediate and delayed benefits of both actors and receivers. It is crucial to develop paradigms that can be used in artificial conditions to investigate these questions carefully. I report here several examples of paradigms used to assess prosocial tendencies in artificial condition, such as the Prosocial Choice Task (PCT), instrumental help and rescue tasks and cooperative tasks.

a) The Prosocial Choice Task

The easiest way to assess prosocial tendencies in animals is to test their propensity to provide food to their partners. The Prosocial Choice Task (PCT) is the main paradigm used to measure prosociality in animals (Silk et al., 2005; Horner et al., 2011). It is a paradigm based on food-provisioning where subjects may choose between different options, usually via token exchanges, or by giving access to a reward to the partner at no supplementary cost. Usually, the actor has two different choices: either the "own reward" choice which provides food to the subject only or the "both rewards" alternative, which delivers food to both the subject and a partner (Hernandez-Lallement et al., 2015). Sometimes a third option with "no reward" is added where no food at all is provided to both participants as a control condition. An

alternative PCT paradigm has been designed where the actor receives no reward in order to avoid the distraction of the food, but in this case, the cost for the donor is increased and their willingness to act prosocial is usually reduced (Jensen et al., 2006; Cronin et al., 2009). It appeared that the presence of visible food disturbed performances of individuals, especially in chimpanzees (Warneken et al., 2007), which could explain their poor performances on previous prosocial tasks. Consequently alternative paradigms with no visible food have been designed to avoid this bias.

Several versions of the PCT paradigm exist. The most common one is using token exchanges (Dufour et al., 2008) or pulling trays (Jensen et al., 2006). Some other experimental set-ups let the possibility to the actor to provide food to a partner, at no supplementary cost, usually while pressing a lever (Lalot et al., n.d) or while opening a baited compartment (Schwab et al., 2012).

The PCT showed prosocial tendencies in many primate species: common marmosets (Burkart, et al., 2007), capuchin monkeys (de Waal et al., 2008, de Waal, 1997), macaques (Massen et al., 2010) and bonobos (Pelé et al., 2009). In our closest relatives, conflicting results have been collected, suggesting that apes like chimpanzees and bonobos were not concerned by others' needs (Tan et al., 2015; Silk et al., 2005; Jensen et al., 2006). Indeed, chimpanzees have been seen for years as reluctant altruists until an experimental study showed that they were able to reward others via token exchanges. These prosocial choices occurred both spontaneously without any solicitation and in response to solicitation by the partner (Horner et al., 2011).

In birds, some attempts to investigate prosociality while using the PCT revealed contrasting results. Ravens (*Corvus corax*) did not demonstrate any prosocial tendencies in a token exchange (Massen et al., 2015a); similar results have been observed with a modified paradigm involving trays to pull: birds did not act prosocial and often ceased to participate when they

did not receive any reward for themselves (Lambert et al., 2017). Another species of corvids, jackdaws (*Coloeus monedula*) had to open a box which was either bated on both sides (for both actor and receiver, prosocial option) or only on the actor's side (selfish option). No significant preference for the prosocial option was spotted but actors were more prosocial when the recipient approached first the box and placed themselves near the reward (Schwab et al., 2012). Finally, African grey parrots have been tested with a paradigm involving four different cups, and could choose to have no reward at all (null) to keep the reward for themselves (selfish), to share the reward with the partner (share) or to donate the reward to the other (giving). Birds acted differently depended on who can choose tokens first and were not eager to share or reciprocate (Péron et al., 2013). In another following-up study, it has been observed that African grey parrots were able to reciprocate favors with the human experimenter (Péron et al., 2014)

b) Instrumental helping and rescue

Another manner to test prosociality in artificial conditions is to test whether an actor will help when there is no benefit for itself. There is no strict consensus protocol but in each situation an actor can help a recipient to do an action that the recipient cannot manage alone: obtain a valuable item or an out-of-reach tool for example, or open a box to give access to a reward, or to free a partner. These actions have been labelled as « targeted help » and suggest that the donor understands the recipient's needs and acts specifically to fulfill these needs.

In most protocols, actors have access to visual cues indicating the receiver's intentions. A study tested dyads of chimpanzees in tool-use situations. Animals were tested in two adjacent rooms, separated by a grid, and each subject possessed the tool that the other needed to solve the task. For example a chimpanzee in the stick-use situation has access to a straw, while its partner in a straw-use situation was provided with a stick. Researchers observed that partners

transferred tool to each other, and that these transfer events occurred to respond to recipients' request (Yamamoto, Humle, & Tanaka, 2009). Another study from the same team demonstrated that a partner was able to choose the tool the recipient needed out of random set of seven objects. Interestingly, this targeted helping (the selection of the right tool) was only possible when the helper had a visual access to its partner's situation. With no visual access, the subject still tries to help but cannot select the right object (Yamamoto et al., 2012). Older studies also revealed that chimpanzees could help other (both conspecifics and humans) at both low-cost and also in costly conditions requiring climbing and maneuvering to retrieve the target object (Warneken & Tomasello, 2006b; Warneken et al., 2007) and can help to retrieve both food and non-edible items (Melis et al., 2011). These experiments suggest that chimpanzees are willing to help others with and without solicitations and they are also able to understand their conspecifics' goals. However more experimental data and evidence were needed in other animal taxa.

Some recent studies investigated rescue behaviors in rats and suggested that helping in these conditions could also be driven by empathy (Ben-Ami Bartal et al., 2011; Ben-Ami Bartal et al., 2014). In these experiments, a rat was trapped in a small Plexiglas restrainer and a partner, free in the arena, was previously trained to open the tube and was able to free its cage mate. Results showed that rats learn quickly to intentionally open the restrainer and free the cage mate, even if social contacts were prevented with the two re-united partners. They opened significantly less empty restrainers or restrainers containing inanimate objects. And when rats had the choice between a restrainer containing chocolate reward and the restrainer with their prisoner cage mate, they usually opened the restrainer with the reward, then freed their partners and shared the food together. The results have been highly debated, and still are (Vasconcelos et al., 2012; Silberberg et al., 2014).

c) Cooperative tasks and taking the other into account

Cooperation, which is a prosocial behavior because it provides benefits to a partner, aroused interest from researchers of many different fields, from psychology, economics, behavioural ecology and ethology. Consequently, many of them tried to define this phenomenon. The definition of cooperation kept in this work is the one proposed by Noë (2006): "all interactions or series of interactions that, as a rule (or 'on average'), result in net gain for all participants. The term includes all other terms that have been used for mutually rewarding interactions and relationships: reciprocity, reciprocal altruism, mutualism, symbiosis, collective action and so forth." In order to better understand the cognitive implications of such behavior and how animals understand the consequences of their actions on themselves and on the others, a study on cooperative hunting in chimpanzees defined several levels of growing complexity of organization between hunters (Boesch & Boesch, 1989): similarity, where all individuals do the same action without any spatial or time relation between them; synchrony, where all individuals do the same action at the same period of time, coordination where all individuals concentrate on similar actions and relate in time and space with each other's actions and collaboration, where individuals perform different complementary action directed towards the same common goal.

To investigate cooperation in controlled conditions, two main paradigms have been used: the "loose-string paradigm" on one hand, where both partners need to pull a string ends simultaneously to obtain the food reward (Hirata & Fuwa, 2007). On the other hand, other studies mostly use the "token-exchange paradigm" where individuals have to cooperate and exchange tokens of different value from one animal to another to obtain a reward and potentially trigger reciprocity. The paradigm is an adaption of the PCT seen above (Dufour et al., 2008; Pelé et al., 2009).

Even if no understanding of the other's actions are required for the first levels of cooperation like similarity (Visalberghi, Quarantotti, & Tranchida, 2000), taking the other into account seems crucial to coordinate and collaborate efficiently (Chalmeau & Gallo, 1995). To assess the understanding of the partner's role, some studies revealed that animals were able to communicate with their partners during a cooperative task, especially with an increase of gaze frequency directed to the other. When confronted to a cooperative pulling task, capuchins monkeys (*Cebus apella*) glanced significantly more to partners than in a control test in which an animal could obtain the reward without help (Mendres & de Waal, 2000). While using a similar sting-pulling paradigm, spotted hyenas (*Crocuta crocuta),* watched partner at the same rate during all the study but they looked at the apparatus more often and showed gaze alternation only during cooperative tests (Drea & Carter, 2009).

Some individuals are able to inhibit their pulling response while they have to wait for their partners to join in a cooperative task, suggesting that they understand the role of the partner (chimpanzees, Melis et al., 2006; elephants *Elephas maximus*, Plotnik et al., 2011; wolves, Möslinger et al., 2009; dogs *Canis familiaris*, Ostojić & Clayton, 2014). However, birds tested while using the loose string paradigm did not delay acting on the apparatus and did not wait for their partners before pulling (rooks *Corvus frugilegus*, Seed et al., 2008; African grey parrots *Psittacus erithacus*, Péron et al., 2011b). Raven did cooperate efficiently, but only when inter- tolerance levels were high and when both participants received equal rewards (Massen et al., 2015b). Keas spontaneously solved the cooperative loose-string paradigm with both human and conspecific partners but they failed both types of control in the training. They paid little attention to the presence or actions of the partner (Schwing et al., 2016). A recent study used a seesaw mechanism with azured-winged magpies (*Cyanopica cyana*); in one of the situations, one bird had to land on a perch to make the reward available for other members of the group, but the actor could not obtain food for itself. Results showed that birds generally

landed first and then waited for another bird to retrieve the reward, suggesting that birds clearly understood their role and the fact that the reward was only available for others (Horn et al., 2016).

6) "Feathered apes" as a model to study prosociality and empathy

Emery & Clayton chose the nickname "feathered apes" to refer to birds from corvids and parrots families because they exhibit developed cognitive (Emery & Clayton, 2004; Pepperberg, 2009) and social abilities (Emery et al.,, 2008; Bugnyar, 2013) comparable to those documented in apes (Emery, 2006 ; Seed et al., 2009 ;Clayton et al.,2007b; Van Horik et al., 2012). Even if they show different types of social organization depending on species, parrots and corvids mostly form fission-fusion groups, as in chinpanzees (Emery, 2016; Juniper & Parr, 1998) and are long-lived species. Consequently they can collect informations about other's relationships and remember partners over a long period of time. A study in ravens demonstrated that they reacted differently to playback of calls from previous group members and unfamiliar conspecifics but also discriminated between familiar birds according to the value of the relationship they had to those subjects up to three years in the past (Boeckle & Bugnyar, 2012). Moreover, individuals have to maintain solid relations with their valuable partner, since they need each other to face opponents and for agonistic support (Fraser & Bugnyar, 2012). In ravens, bystanders console victims with whom they share a valuable relationship, reducing the victim's post-conflict distress (Fraser & Bugnyar, 2010a; Fraser & Bugnyar, 2010b). Corvids are known both for their complex social lives and the maintenance of affiliative relationships and alliances within their groups in addition to their pair bonds (Fraser & Bugnyar, 2010b; Bugnyar, 2013; Boucherie et al., 2017). They are also know to be involved in social play (Diamond & Bond, 2003 ; Auersperg et al., 2015; O'Hara & Auersperg, 2017). Several bird groups, e.g. corvids and parrots, live in individualised societies comparably complex to those of primates (Emery, 2004; Emery, Clayton, & Frith,

2007). Rooks *Corvus frugilegus* (Boucherie et al., 2016, 2017), jackdaws *Coloeus monedula* (von Bayern et al 2007), ravens *Corvus corax* (Bugnyar, 2013) and parrots (Garnetzke-Stollmann & Franck, 1991) for example show similar affiliative association patterns than primates, such as sitting in proximity, allopreening and allofeeding. Preferential affiliative associations occur between sexual partners (Rogers & McCulloch, 1981; Wechsler, 1989), since corvid and parrot species but also anatidae like geese (Black, 2001) in particular form strong long-term monogamous pair bonds (Emery et al., 2007), but affiliative relationships are also observed between siblings (Wanker et al., 1996) and between unrelated individuals of the same sex (Fraser & Bugnyar, 2010b; Boucherie et al., 2017). In corvids (von Bayern et al., 2007; Loretto et al., 2012) and parrots (Wanker et al., 1996; Stamps et al., 1990; Lievin-Bazin et al. n.d), juveniles indeed exhibit strong bonds with their siblings. However, when becoming adults, most corvid and parrot species, mature individuals usually pair up with a single mate, i.e. only maintain a single strong affiliative bond and, hence, their mate becomes their preferred partner (Emery et al., 2007; Mock & Fujioka, 1990). Such long-term pair-bonded birds show many interactive behaviours exclusively with their mate such as allopreening and allofeeding (Röell, 1978; von Bayern et al., 2007; Wechsler, 1989; Rogers & McCulloch, 1981).

The latter, i.e. affiliative relationships other than between mates, may be less stable. Wild non-breeding ravens, for example, typically do not maintain affiliative relationships over a long period of time (Braun & Bugnyar, 2012). Such extra-pair affiliative relationships may serve a strategy to find a new mate, which may be gradually transformed into a stable pair bond (Boucherie et al., 2017). Forming affiliative associations with mates or non-sexual partners can be rewarding in many ways. It may provide better access to food (Fraser & Bugnyar, 2010b) or support in conflict situations with other group members/conspecifics

(Fraser & Bugnyar, 2012). Partners may also cooperate through coalition formation (Loretto et al., 2012) or by providing consolation following stressful situations (Fraser & Bugnyar, 2010a).

Contrary to primates, which are generally polygamous, corvids and parrots form long-term monogamous pairs and it has been suggested that long-term monogamy comes with an attachment driven by emotion (Black, 1996). Some previous work evoke a psychological bond between partners which may result from a common attachment to territory, a familiarity of each other created after a long period of proximity or something akin to human affection (Welty & Baptista, 1988). Since pair-bonding in monogamous birds can last for a very long period of time, members of a mated pair share a complex history of interactions, experiences and emotions (von Bayern, 2008). Some anecdotal observations done on species involved in life-long bonding seem to indicate the existence of this emotional part too. For example, some behavioral displays apparently associated to grieving have been reported in geese after the death of a lifelong mate (Lorenz, 1966). Even if some neurological studies are needed to correlate that kind of behavior to brain structures activation (like hippocampus) and emotions, these findings arise many questions about partner attachment and the nature of this link.

Corvids and parrots also exhibit developed cognitive abilities. Both corvids (magpies *Pica pica,* Pollok et al., 2000; Eurasian jays *Garrulus glandarius,* Zucca et al., 2007) and parrots (African grey parrots *Psittacus erithacus* & parakeets, Pepperberg et al., 1997, Pepperberg & Funk, 1990a; Goffin cockatoos *Cacatua goffiniana,* Auersperg et al., 2014b) possess object permanence and could follow the displacement of invisible objects.

Some corvids like western scrub-jays *Aphelocoma californica* (Clayton et al., 2007a) and ravens (Bugnyar, 2007) also possess the ability to take others' mental states into account, which are high-cognitive abilities associated with Theory of mind (Premack & Woodruff, 1978) and mainly observed in primates. Many of the Theory of Mind studies in corvids

include food-caching paradigms. Ravens have been shown to recache food more often when observed by a conspecific and are able to infer perceptual access of others (Bugnyar et al., 2016). They are also capable of deception and can lead a partner away from a food source (Bugnyar & Kotrschal, 2004). Ravens are also able to plan for tool-use and barter with a human experimenter with delays of up to 17 hours in order to obtain food (Kabadayi & Osvath, 2017). Western scrub-jays can remember who was watching and when, while they were caching food (Dally et al., 2006). They are then able to recache depending on the state of knowledge of their observer, to plan for the future and cache food in prevision of the next morning (Raby et al., 2007). They are also able to choose food depending on the time the food was cached: they choose to retrieve non-perishable food after a long waiting period even if it is the less preferred food (Clayton et al., 2003). Some other recent studies in European jays (*Garrulus glandarius*) demonstrated that long-lasting sexual partners are also able to infer mental states and desire of their partner in a food-sharing context. Male were able to determine the food the female would preferentially eat depending on the food she previously ate (Ostojić et al., 2013).

Until now and even if these results are still highly debated, only European magpies (*Pica pica*), which are part of the corvids family, did recognize themselves in the mirror and passed successfully the mirror-mark test (Prior et al., 2008). These results suggest that these birds could make the self-other discrimination which is a crucial ability to exhibit empathic behavior (Bischof-Köhler, 2012). A study in young human children showed that only subjects being able to recognize their mirror reflection could provide support to an experimenter showing distress (Bischof-Köhler, 1991).

Moreover, some corvids and parrots are very talented to use tools and could even learn to manufacture them in captivity, while it is not a behavior they express in the wild, like in ravens (Kabadayi & Osvath, 2017) or rooks *Corvus frugilegus* (Bird & Emery, 2009). It is

also the case of Goffin cockatoos who used and manufactured tools spontaneously in captivity (Auersperg et al., 2012) and can also transmit their tool-related knowledge via social transmission (Auersperg et al., 2014a). New Caledonian crows (*Corvus moneduloides*), which are natural tool- users are also able to shape hooks from raw material (Weir et al., 2002) and to construct different type of tools (Hunt, 1996; Hunt & Gray, 2004).

Until now, many studies have investigated food-sharing in avian social groups of members of the corvid family, i.e. jackdaws (de Kort et al., 2006; von Bayern et al., 2007), pinyon jays *Gymnorhinus cyanocephalus* (Duque & Stevens, 2016), ravens (Boeckle et al., 2012) and rooks (Scheid et al., 2008; Boucherie, 2016). A much less studied group of birds, the order of Psittaciformes, including parrots and parakeets, shares several life history characteristics with corvids and they appear to exhibit comparable cognitive capacities (Osvath et al., 2014).

These numerous evidences suggest that corvids and psittacids are especially good candidates to investigate the link between social relationships, prosociality and empathy.

III) Biological models: general presentation

In this Thesis, both corvids and parrots were involved in this work: five species of parrots and parakeets and one species of corvids have been experimentally tested. All birds studied were captive: all psittacids were birds born in captivity while jackdaws were wild born, have been removed from the nest when they were nestlings and have been hand-raised by humans.

Even if they live in different ecological environment, and have different diets, parrots and corvids share many similarities. They are long lived, large-brained, have a long developmental period before being matured, live in social groups with fission-fusion dynamic, form long-term monogamous pair bonds and are already known for their complex cognitive abilities, their flexible behaviors and abilities to solve complex problems.

1) Psittacids

a) Cockatiels (Nymphicus hollandicus)

Figure 1. From left to right: Viviane, Hermès and Sita, three cockatiels from Nanterre's colony. Photo: G. Huet des Aunay

Cockatiels are small nomadic parakeets endemic to Australia. They are living in arid and semi-arid areas in pairs or flocks up to 100 birds and are forming long-lasting pair-bonds (Juniper & Parr, 1998). They feed mainly on seeds. Even though they are one of the most familiar pet parrots and a common cagebird all around the world (since the end of the 18th century), they have not been much studied as biological models of avian cognition yet. To our knowledge, the only behavioral studies on cockatiels until now focused on reproductive behavior (Myers et al., 1988; Millam et al., 1988), egg productions (Millam et al., 1996), mate compatibility (Spoon et al., 2004; Yamamoto et al., 1989) and gender effects on aggression, dominance rank and affiliative behaviors (Spoon et al., 2004; Seibert & Crowell-Davis, 2001). A case study investigated if one single individual of 8 months old possessed an object

permanence, and was able to retrieve hidden objects and follow object movements, which was demonstrated in the experiment (Pepperberg & Funk, 1990b). Some other studies investigated taste perception in this species (Matson et al., 2001) and personality traits, once again to maximize reproductive success for breeders (Fox & Millam, 2010; Fox & Millam, 2014).

b) African grey Parrots (Psittacus erithacus)

Figure 2 African grey parrot during preening.
Photo: Wikipedia creative commons

African grey parrots live in primary and secondary rain equatorial forest and wooded savanna in Africa (Guinea-Bissau to Tanzania). They mainly eat fruits and seeds. They are social birds which also live in large flocks, join during mobbing events and form long-term monogamous pairs (Jones & Tye, 2006). Irene Pepperberg's pioneer works on Alex the famous talking parrot provided us some precious insights on these birds developed cognitive abilities (Pepperberg, 1990), which have been since completed by more recent works. Grey parrots are

known for their functional vocalizations associated with the acquisition of complex concepts such as same/different, shapes, colors, numbers (Pepperberg, 1981, 1983, 1987a), their numerical abilities (Pepperberg, 1987b, 1994) and their ability to distinguish several quantities (Al Aïn et al., 2009). They are also able to cooperate in artificial tasks (Péron et al., 2011b), to act prosocial with a conspecific or with an human experimenter, depending on this human behavioural attitude (Péron et al., 2013, 2014) and to adapt their responses according to the experimenter's intentions (Péron et al., 2010).

c) Blue-throated macaws (Ara glaucogularis)

Figure 3. Pair of blue-throated macaws. Photo: Wikipedia creative commons

Macaws are large birds (80-96 cm) living in South-America. Blue-throated macaws are endemic to small areas of western Amazon basin (Yamashita & de Barros, 2013). They generally live in long-term pairs and are less gregarious than other parrot species. They also mainly eat fruits and seeds. The juveniles stay with their parents only for a brief period of

time. This is probably why so few family parties are observed together in the wild (Juniper & Parr, 1998).

d) Scarlet macaws (Ara macao)

Figure 4. Scarlet Macaw. Free image from Pixabay

Scarlet macaws are the most widely distributed (Mexico to Brazil) of the 17 extant macaw species (Vaughan, Bremer, & Dear, 2009), they live in lowland tropical forests and savanna. They are cavity-nesters and form long-term monogamous pairs. They usually form small groups, as they are gregarious birds like most members of the parrot family. Their diet is the same than other parrots, and they mainly eat fruits and seeds.

e) Sun conures (Aratinga solstitialis)

Figure 5. A pair of sun conures. Photo: Pixabay

Sun conures are small parakeets, distributed in North-eastern South America. Their habitat is restricted to dry, semi-deciduous forests. They also eat fruits and seeds, form long-term monogamous pairs and live in flocks of up to 30 birds (Juniper & Parr, 1998).

To our knowledge, no behavioural experimental studies involving these three species of parrots have been ever published yet. Most publications investigate their protection and conservation status (Brightsmith et al., 2005; Guedes, 2004), reproductive success (Berkunsky et al., 2014) genetic analyses for reintroduction and taxonomy (Nader et al., 1999; Ribas & Miyaki, 2004; Silveira et al., 2005; Lucca, 1984) or veterinary reports of disease (Kerski et al., 2012). Only one PhD thesis investigated cooperation in a flock of green-winged macaws (*Ara chloroptera*) via several lever paradigms (Spitzhorn, 2009).

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2) Jackdaws

Figure 6. Jackdaws from the 1st aviary in the Avian Cognition Lab. Photo: Agatha Liévin-Bazin

Just like parrots, jackdaws form social dynamic groups called colonies in which several long-term monogamous pairs aggregate together, live in proximity and cooperate to mob predators. Jackdaws are opportunistic, they eat fruits, seeds, eggs and meat (small invertebrates, rodents, roadkills; Lockie, 1955) and are found through all Europe, loving to nest at the top of buildings, churches and towers as they are cavity-nesters. Jackdaws are small highly social and long-term monogamous corvids that typically breed in colonies (Röell, 1978).

Contrary to parrots and parakeets whose social and physical cognition have been rarely studied, jackdaws have been observed since the 1930's by Konrad Lorenz, who investigated their linear hierarchical group structure, with pair-bonded birds sharing the same rank (Lorenz, 1931). Some other recent studies investigated dominance, hierarchy and their consequences in term of fitness in jackdaws. Exploration of both novel object and novel space

seems also linked to the social structure of the group : in each social group, some birds initiated the approach and exploration of novel space and/or objects but interestingly top-ranking birds did not act as initiators, suggesting that dominants are more conservative (Katzir, 1982; Katzir, 1983). A more recent study demonstrated that dominants birds have low fitness because it is costly to be on top of the hierarchy. Dominant males produced fewer nestlings, which had lower chances of survival to 1 year of age (Verhulst & Salomons, 2004).

Jackdaws are also especially renowned for their social association and the strength of their bonds (Kubitza et al., 2015; Wechsler, 1989). Mates form strong associations, are very competitive for resources with other mated pairs, especially for nest sites, and a strong cooperation arises between mated partners to protect their nest from intruders during the breeding season (Röell & Bossema, 1982). They are known to form strong, exclusive and long-lasting monogamous pair bonds (Wechsler, 1989; Henderson et al., 2000; Kubitza et al., 2015), in which partners cooperate to monopolize nests and raise nestlings (Röell & Bossema, 1982). Like many corvids, jackdaws have been reported to be highly neophobic (Katzir, 1982 ,1983; Greggor et al., 2016) and, appear very sensitive to conspecific gaze (von Bayern & Emery, 2009;Davidson et al., 2014). They are also able to recognize different human individuals and to differentiate a threatening mask from a neutral one and adapt their behavior accordingly to protect their nest and chicks (Davidson et al., 2015) and appear to respond to human's attentional states (von Bayern & Emery, 2009).When tested in a social facilitation task with objects, juvenile jackdaws seemed to attend more to the objects non-affiliated conspecifics had interacted with than to those that affiliated individual had explored (Schwab et al. 2008a).

Jackdaws's tendency to act prosocial has also been investigated. A study tested the ability of jackdaws to reward a partner in a prosocial task with different reward options: prosocial (both birds received a reward), altruist (only the receiver had food), selfish (only the donor received

food) or null (no reward). Donors had to open a box which was either baited on both sides (for both actor and receiver, prosocial option) or only on the actor's side (selfish option). Result showed that the recipient's behaviour affected the donor's choice. Indeed, actors were more prosocial when the recipient approached first the box and placed itself near the reward, than when actors approached first. And donors were more prosocial or altruist with opposite-sex partners (Schwab et al., 2012). The same team also examined the link between social learning and the relationship between the demonstrator and the observer. Surprisingly, jackdaws did not learn from any conspecific or learned from either non-siblings or non-pair partners when bonded, which suggested that affiliates spend so much time together in proximity that they learn and experience the same things at the same moment and do not need to pay even more attention to each other to gain information about their foraging strategies. More distant individuals, experiencing other situations are more likely to provide new information (Schwab et al., 2008a)

As other corvids, like ravens, jays or magpies, jackdaws have been suspected to possess theory-of-mind-like abilities, because their complex social associations involved to always be in close proximity with other pairs and potential competitors. This means that they have to keep tracks of movements and interactions of others to protect their own resources and know with whom forming alliances. Nevertheless, they did not cache much food in the wild (Henty, 1975) so they could not been tested with the same experimental paradigms involving caching strategies as ravens and jays. However they seem to be able to infer perceptual states and intentions in another species: humans. Indeed, a recent study showed that jackdaws were able to distinguish different human individuals and could also differentiate intentions of these observers, wearing human face mask, depending on the position of these masks. They adapted their behaviour and responded with defensive behaviour if the gaze cues (the eyes of the mask) were directed towards their nest (Davidson et al., 2015). Moreover, jackdaws are able

to follow a human experimenter's gaze direction, which is a complex ability, especially when it implies a signaller and a receiver from two different species (von Bayern & Emery, 2009). They are also one of the rare bird species which have been tested for the mirror-mark task, but until now, no sign of mirror-self recognition has been shown in this species (Soler et al., 2014).

Jackdaws have also been tested in prosocial tasks. A study in young jackdaws showed that active giving, as a costly signal, promoted and strengthened bonds between individuals and also seemed involved in pair bond formation (von Bayern et al., 2007). Indeed, the birds that shared food during the 3 months period following fledgling, became increasingly selective until they exclusively shared food with only one partner, who usually became their mate. Consequently, the proportion of food exchanged and the number of dyads involved in food-sharing decreased over time, after a peak during the 2-3 months period post fledging. The same pattern of food giving has been observed in another population of captive jackdaws (de Kort et al., 2006). This decrease over time could indicate the functional aspect of food-sharing in pair bond formation, since young jackdaws choose their lifelong mate very early in their life, usually in their first autumn (Lorenz, 1931)

All these results suggest that jackdaws possess a complex social life and that the strong affiliations between individuals may play an important role in reinforcing and maintaining it over time.

IV) Aim of this Thesis

As described earlier, the scientific community recently showed a growing interest for emotional and social life of animals and the cognitive underpinnings of these behaviors. Recent discoveries also made us understood that other animal taxa, like birds, possess apes-like abilities in managing social complexity and problem solving in a changing environment.

The aim of this Thesis is to investigate the role and implication of social relatedness and affiliation in prosociality and empathy in "feathered apes", parrots and corvids, the two families of birds with the most advanced cognitive abilities presently known. I investigate the existence (or the absence of evidence) of prosociality in psittacids, since only few studies have been conducted with these birds. I also evaluate the emotional connectedness between individuals in both parrots and corvids. I concentrate on the transmission of negative emotions from one individual to another and the behavioral responses of individuals when put in a stressful situation with or without their preferred partners.

In the first study, I report the results of a developmental study on both food-sharing and affiliative behaviors in young cockatiels over a 3 years period. We investigated whether food-sharing, which is a prosocial behavior, could be used as a costly signal to choose a reliable mate and to form early pair-bond affiliations. This experiment was a replication of a paradigm used with young jackdaws by Auguste von Bayern, my german PhD supervisor. We studied if similar patterns could be observed in these two evolutionary distant species sharing many similarities in their ecology and behaviors. The degree of affiliation and the way preferential links between individuals evolve other time were also investigated. Our aim was to run a longitudinal study of food-sharing in young cockatiels peers over a 3 years-period of time, which is longer than previous similar studies (Scheid et al., 2008; von Bayern et al., 2007). We extended the von Bayern et al (2009) study on jackdaws, using the same methodology

even though cockatiels were older than jackdaws when the experiment started. We were interested to see whether a similar developmental pattern would be observed in cockatiels as in jackdaws and if the food-sharing between juveniles similarly would predict pair-bond formation in adults. In this study, the birds were observed at four distinct periods, i.e. from a young age (around 9 months old) until the moment they reached sexual maturity (over 2 years old) and we focussedon both their food-sharing as well as their affiliative behaviour.

In the second study, I investigated the existence of emotional contagion, the simplest level of empathy in cockatiels and quantify the behavioral responses of birds to a stressful stimulus (distress calls) depending on the level of affiliation shared between the emitter of the calls and the receiver of the calls (the subject). I chose to study the behavioural responses of cockatiels (*Nymphicus hollandicus*), a highly social, long-term monogamous species, belonging to the cockatoo family, to conspecific distress calls of varying degree of affiliation. Cockatiels exhibit a rich vocal repertoire and should be capable of individual vocal recognition (Saunders, 1983). We exposed individuals to a control sound (white noise) and to two types of distress calls: the distress call of a partner, a bird with which the subject maintained a strong affiliative bond, and the distress call of a non-partner, a familiar bird housed in the same aviary but which shared no particular relations with the subject. Our goal was to investigate whether the degree of affiliation between individuals, would be reflected in the strength of the behavioural response of the subjects. We recorded and analysed the behavioural responses of the birds to the different stimuli described above, before, during and after playback stimuli, expecting that the birds would show the strongest response to distress calls by their partners and would also respond but to a lesser degree to those of other group members. It is, to our knowledge, the first study investigating emotional contagion towards the response to conspecific distress calls depending on affiliation in birds. My hypothesis is that subjects

sharing a strong affiliation would react more intensively to the distress calls of their partners, than to the calls of their non-partners.

In the third study, I present three experiments investigating prosociality via a Prosocial Choice Task involving token exchanges in four species of parrots: *Ara glaucogularis*, *Ara macao*, *Aratinga solstitialis* and *Psittacus erithacus*. In the first experiment, birds were tested for their propensity to reward a partner at no supplementary cost by choosing one object among a set of the three available items via the PCT paradigm. This experiment investigated the existence of prosociality in these species by studying whether parrots preferred outcomes that benefited a partner over outcomes that provided no benefit to it. We selected individuals sharing preferential bonds to participate in this experiment. Macaws and parakeets were tested with their mates or their siblings. Each bird had only one preferred partner in testing session, except in the case of African grey parrots, which were tested with two different partners. In this case, we expected that the relationship between the birds would influence their behaviour and preferences. According to their tolerance and previous interactions, they could be more or less willing to reward their partner.In the African grey parrots group two individuals (a male and a female, Léo and Zoé) were very tolerant to each other, but a third parrot (a male, Shango) sometimes displayed aggressive behaviour toward the female.

In the second experiment, we used the same PCT paradigm than in the first experiment but we introduced inequity, in order to see if prosociality would be damaged. In this experiment, we randomly alternated both control and iniquity condition, in which the partner received a more attractive reward than the subject when it picked up the “both reward” object. Therefore, as seen in primates, we expected the donor to develop a preference for the “own reward” option or to stop participating.

In the third and last experiment, the subject had to choose one token, then transfer it to the partner, and the partner had to give it to the experimenter to obtain a reward. As in the two previous experiments, the partner only received a reward when the subject chose the "both reward" option, but in this case, the subject could only have a reward if the partner cooperated. If the subject chose the "own reward" object, which would not reward the partner, and if the partner refuse to cooperate and did not give the token to the experimenter, the donor would not receive any reward either. The subject was expected to adapt its choice according to the behaviour of its partner, since the willingness of the partner to cooperate, would influence the rewards the donor could possibly obtain. We hypothesized that the subject would preferentially choose the prosocial token.

Even if no direct reciprocity could be assessed because birds did not take turns after each trial, general strategy matching within a dyad could emerge in the first two studies.

In the fourth and last study, I observed behavioral responses and exploration of jackdaws when confronted to scary novel objects and I investigate the impact of the partner's presence on these behaviors. The aim of this study was to investigate whether the neophobic response and exploratory behavior of jackdaws exposed to several novel stimuli, differed depending on the social context, and whether it was affected by the relationship shared with a familiar conspecific. We tested jackdaws in three social contexts, i.e. alone, with their partner (i.e. mate) or with an opposite-sex non-partner, and exposed them to five conditions. In a control condition, they were presented with a food bowl filled with a small quantity of desirable food. In the four other conditions they faced the bowl and amount of food but also different novel objects of varying size and averseness: small plush toys, plastic bath toys, moving toys mimicking the movement of an insect, very small plastic toys and images of predator's eyes. Assuming that stress may be alleviated by social contact, we hypothesized that the birds'

neophobic response (i.e. the approach latencies) may be reduced in the presence of a conspecific and further diminished when the conspecific is the subject's partner, while concurrently increasing the subjects' propensity to explore the novel object. I also wanted to see if some reassuring behaviors could be observed between partners in this stressful situation.

Material and methods

Matherial and methods

Ethical statement

Cockatiels

All the birds were housed in standard conditions approved by the French National authority. This study complies with French and European legislation for animal care and was approved by the Ethical Committee for Animal Experimentation Charles Darwin (authorization number 2015031616168767 v6 (APAFIS#344)).

African grey parrots, conures and macaws

Data collection was carried out in accordance with the U.K. Animals (Scientific Procedures) Act, 1986 and associated guidelines, EU Directive 2010/63/EU for animal experiments and the National Institutes of Health guide for the care and use of Laboratory animals (NIH Publications No- 8023, revised 1978).

All the birds were housed in standard conditions approved by the French National authority. African grey parrots were kept after the experiment in the laboratory at Nanterre university and participated in other tests. The other birds stayed at the "Ferme de Conservation Zoologique".

Jackdaws

The study was conducted in accordance with national and EU legislation and guidelines for animal research. According to German law, the study was considered non-invasive and therefore not classified as an animal experiment.

Subjects and housing conditions

Cockatiels

Cockatiels (*Nymphicus hollandicus*) were tested in the first study on food-sharing and in the third study presented in this thesis, which investigated emotional responses to conspecific distress calls.

A flock of thirteen young cockatiels (6 females and 7 males) was used in this thesis. Only ten birds were tested in the food-sharing and emotional response studies, but the tested individuals were different in study 1 and 3 (Table 1). This flock can be divided in three subgroups that did not interact much with each other but within which individuals were affiliated: first two sub-groups, seven birds in total, arrived in the laboratory in October 2013. One of them consisted of siblings (Bahloo, Rama, Merlin, Nephtys and Seth) and did not interact much with other subgroup which was composed of unrelated birds (Wala, Sita, Callisto, Hermes, Viviane). Three further unrelated birds (Odin, Skadi and Loki) formed the third subgroup that arrived one year later. This second unrelated subgroup did not interact much with the other birds in the aviary either. Rama died during the first study in August 2014 and could not be tested in other experiments.

The two first subgroups were brought together in a single colony in February 2014. The three last birds (Loki, Skadi, Odin) joined the other two subgroups within the same aviary in February 2015

All birds hatched in captivity and arrived at the Laboratoire Éthologie Cognition Développement in Paris-Nanterre University between three and five months of age either in October 2013 (for the 10 first birds) or in September 2014 (for the last three birds). Birds were provided by two different breeders. The first subgroup was composed of siblings, while the other birds were unrelated birds. Siblings presented two different colour morphs: three of them (Nephtys, Seth and Merlin) were Cinnamon pied cockatiels while the two other brothers

Rama and Bahloo were Silver types. They were hand-raised by human and were housed with juveniles of other species before arriving in the lab. Unrelated birds were more dissimilar and presented 5 different colour morphs. Unrelated birds were all issued from different nests and raise naturally by their parents but were also manipulated by the breeders to habituate them to humans. The sexes of each young bird were assessed by genetic analysis using feather samples. Each bird was identified by a specific metal ring.

All birds were housed together in an indoor aviary (296 cm x 257 cm x 257cm) equipped with three stainless steel tables (155 cm x 55 cm x 84 cm) covered with Kraft paper, two large perch structures (2 meters long), two triangular bird swings hung from the roof and many parrot toys. The room was kept on an automated light:dark cycle (time on: 09:00, time off: 19:00) with UV daylight tubes especially designed for birds (Arcadia Bird lamp T8). The temperature was maintained at 25 C°. Extrudes granules (Nutribird G14), anise sand, fresh fruits, vegetables and water were provided *ad libitum*.

Birds	Sex	Subgroups	Relations	Date of arrival in the lab	Present in study
Bahloo	M	1	Siblings	October 2012	1
Rama †	M	1	Siblings	October 2012	1
Merlin	M	1	Siblings	October 2012	1
Seth	M	1	Siblings	October 2012	1 & 2
Nephtys	F	1	Siblings	October 2012	1 & 2
Callisto	F	2	Unrelated birds	October 2012	1 & 2
Wala	F	2	Unrelated birds	October 2012	1 & 2
Sita	F	2	Unrelated birds	October 2012	1 & 2
Viviane	F	2	Unrelated birds	October 2012	1& 2
Hermès	M	2	Unrelated birds	October 2012	1 & 2
Loki	M	2	Unrelated birds	September 2014	2
Odin	M	2	Unrelated birds	September 2014	2
Skadi	F	2	Unrelated birds	September 2014	2

Table 1. Characteristics of cockatiels used in the experiments of this thesis: names, sex (M: male; F: female), relations, date of arrival in the lab and participation to study 1 (food-sharing) and/or study 2 (emotional responses to conspecific distress calls). † Cross indicates bird that died during the study.

Other parrots

Other parrots as African grey parrots, conures and macaws were used in the second study of this thesis in order to investigate prosociality in an experimental artificial task in these birds.

Nine parrots from four different species were used. On one heand, we tested: three African grey parrots (*Psittacus erithacus*) housed in the Laboratoire Éthologie Cognition Développement at Paris-Nanterre university and, on the other hand, two blue-throated macaws (Ara glaucogularis), two sun conures *(Aratinga solstitialis*) and two scarlet macaws (*Ara macao*) housed at the "Ferme de conservation zoologique", a small private park dedicated to conservation and located in Mery-sur-Cher, France.

African grey parrots participated to all experiments. Other parrots were only involved in the first experiment and were exclusively tested with their sibling or their mate. It was unfortunately impossible to involve them in the two other experiments since more interaction with experimenters and apparatus were needed.

a) <u>African grey parrots</u>

We tested three hand-reared African grey parrots: one female (Zoé, six years old) and two males (Léo and Shango, six and four years old respectively). The three birds were tested in the first two experiments. In the second experiment involving inequity condition, the tested dyads (with switching roles) were: Zoé-Léo (female-male), and Léo-Shango (male-male). The dyad Shango-Zoé (male-female) was not tested because of agonistic interactions. This experiment lasted one month and was conducted just after the last replication of the first experiment. In the last experiment, only the two males have been tested: Shango and Léo. Léo played the role of the subject, the bird who had to choose the item. We couldn't switch roles as initially planned because Shango died only a few weeks after the end of this experiment. This experiment has been done one year after the end of the second experiment about inequity

and lasted approximatively two months. Zoé did not participate in this experiment because of health issues. She was moved to another room where food and toys were provided during the sessions.

African grey parrots hatched in captivity and arrived at the laboratory in Paris-Nanterre University at three months old. They were housed together in an aviary (340 cm × 330 cm × 300 cm) with three tables (120 × 60 × 75 cm), two large perch structures and many toys. The aviary was maintained at a constant temperature of 25°C and a 12/12 h light-dark cycle. Dyads were tested in the aviary while the third bird was placed in a cage in the corridor with food and toys. The parrots were fed with fresh fruits and vegetables in the morning and parrot formula (Nutribird A21) in the evening. Water and parrot pellets (Harrison, high potency coarse) were available *ad libitum* and vitamins (Muta-Vit Versele-Laga) were given twice a week.

b) Conures and macaws

The other parrots were tested at the 'Ferme de Conservation Zoologique': two two-year-old blue-throated macaws forming a mated pair (*Ara glaucogularis*), two one-year-old male siblings sun conures *(Aratinga solstitialis)* and two ten-year-old scarlet macaws also forming a mated pair (*Ara macao*).

The *A. glaucogularis* pair was formed for only one year and never laid eggs before being tested while the *A. macao* pair had already mated together. The two males *A. solstitialis* were hand-reared together and shared a cage with six others family members. The birds were housed in aviaries (indoor: 2 x 2 x 2 m & outdoor: 5 x 2 x 2 m) with various enrichment devices (wood blocks and plastic toys) and were fed *ad libidum* with seeds (Verse Laga Premium), parrot pellets (Verse Laga P15), fruits vegetables and fresh water. All birds were tested in their aviary apart from the breeding season. As subjects were free-flying parrots, all

test sessions were based on their motivation. Indeed, the birds could leave at any time and perch elsewhere in the aviary during test sessions.

Jackdaws

Twenty individually banded, hand-reared jackdaws kept in two groups by the Max Planck Institute for Ornithology, Seewiesen, Germany were tested. Each group was composed of five mated pairs (five males and five females for each group).They were housed in two adjoining large outdoor aviaries.

Jackdaws were housed in two large outdoor group aviaries Group 1: 15 m × 9 m × 2.8 m; Group 2: 12 m x 10 m x 2.80 m) including testing compartments (2 m × 3 m × 2.8 m each) and were provided with plenty of perches, natural substrates and hiding-places. Subjects had been trained during previous experiments to enter test compartments and were used to participate in brief behavioural tests in visual isolation of other group members.

The birds were fed in the morning with a diet consisting of cereals, fresh fruit, a meat mixture containing, curd, boiled rice, egg, dried insects, oils, vitamins and minerals, as well as soaked cat biscuits, which was available ad libitum during the entire day. They also had constant access to fresh water.

Study 1: Food sharing in cockatiels

10 young cockatiels (see Table 2) were tested in this study at four different periods of time during three years, from first months of life to adulthood

Individual	Sex	Subgroup	Age at Period 1 (in months)	Age at Period 2 (in months)	Age at Period 3 (in months)	Age at Period 4 (in months)	Present in period
Bahloo (B)	M	Siblings	7	8	15	30	1,2,3,4
Rama (R) †	M	Siblings	7	8	/	/	1,2
Merlin (M)	M	Siblings	7	8	15	30	1,2,3,4
Seth (S)	M	Siblings	7	8	15	30	1,2,3,4
Nephtys (N)	F	Siblings	7	8	15	30	1,2,3,4
Callisto (C)	F	Non-kin	9	10	17	32	1,2,3,4
Hermès (H)	M	Non-kin	9	10	17	32	1,2,3,4
Wala (W)	F	Non-kin	10	11	18	33	1,2,3,4
Viviane (V)	F	Non-kin	10	11	18	33	1,2,4
Sîtâ (Si)	F	Non-kin	11	12	19	34	1,2,3,4

Table 2 **Characteristics of the subjects**: identity of the birds with their names and abbreviations resumed by letters, sex (F: Female; M: Male), subgroup and age at period 1, 2, 3 and 4 in months. All birds were housed together but formed two distinct subgroups. The first subgroup was constituted of siblings (N, B, R, S and M) and the second subgroup of unrelated birds, sharing no kin relationships (H, Si, V, W, C). † Cross indicates bird that died during the study.

Experimental feeding trials

The present study was a longitudinal developmental one, performed over three years. Birds were tested at 4 different ages in 4 periods of time: between April 24th and May 9th 2014 (period 1); between May 30th and July 04th 2014 (period 2); between February 18th and March 04th 2015 (period 3) and between June 20th and July 01st 2016 (period 4). The birds were respectively 7-11 months old during period 1, 8-12 months old during period 2, 15-19 months old during period 3 and 30-34 months old during period 4.

Following the methodology used in studies on corvids (jackdaws; *Coloeus monedula*) by de Kort et al (2006) and von Bayern et al (2009), each cockatiel received 14 feeding trials per testing period: 7 trials with a preferred type of food (fennel) and 7 trials with a less preferred type of food (carrot). The preference had been established via a food preference test conducted before the experiments and revealed that fennel was significantly preferred over carrot when equal amounts of both food types were offered to the birds simultaneously. During every trial, each bird was given 10 pieces of food (ca. 0.3 cm x 0.5 cm) consecutively. The experimenter held the food piece between two fingers and reach out towards the bird which had to pick it up. The food was handed out piece by piece to each bird. The experimenter waited for the bird to consume entirely the food piece, to drop it or to transfer it to another bird before giving him the next food piece. The focial bird should have its beak empty before each single trial. All birds were free to move during when the target bird was provided with food and we did not keep them away from the subject, to see how birds will interact during the feeding. The type of food, fennel or carrot, alternated between trials. Cockatiels did not receive those two food types outside the feeding trials and they were food-deprived approximatively 2 hours before the beginning of each trial. Birds were tested once or twice a day, with one trial being conducted in the morning and another trial in the afternoon. The order in which individuals received the food items was randomized for each trial.

Overall, i.e. across the 4 periods, each bird received 560 food pieces except for two birds. One of them, the male Rama, died of illness a few months after the second period of testing and another individual, the female Viviane, refused to take the food during the third period of testing.

One experimenter gave the food pieces to the birds while a second experimenter held the camera and recorded the focal bird's behaviours.

For each food item provided to a focal bird, we recoded whether the bird ate the item (consuming), dropped it on the floor (dropping), shared the item with another individual, i.e. jointly eating from the same piece of food (cofeeding) or had the item stolen by another bird, i.e. snatched from the beak from the focal bird, involving aggressive behaviors (stealing). When stealing occurred, we recorded whether aggressive behaviours such as pecks or threat displays (when a bird opened the beak to displace another) were observed from the focal bird, the potential receiver or both individuals before and/or after the food exchange. Instances of cofeeding on the contrary involved no aggressive behaviors before and/or after the food exchange. During cofeeding, the target bird usually kept the food item in his beak while another bird nibbled from it. In both conditions, a food transfer took place from the beak of the donor to the beak of the receiver. In some rare cases, the focal bird exchanged food with a first receiver, which then passed on the food item to a second receiver. Even if these events were recorded, only the exchange between the focal bird and the first receiver were analysed. With difference to the previous studies on jackdaws (de Kort et al., 2003; von Bayern et al., 2007), it was not possible to distinguish between donor-initiated and receiver-initiated food transfers because, the cockatiels showed no clearly distinguishable behaviours indicating their motivation to share or beg for food. Only one strategy was analyzed per trial.

Trials were recorded on a camera (Sony Handycam HDR-CX410) on a tripod (Vanguard Mak 203). Videos were analysed using the software VLC media player, version

1.5. and “strategies” (the destiny of each food item) were determined during video coding. Each video was analysed by two different experimenters in order to ensure inter-observer reliability.

Degree of affiliation

All birds were group-housed in the same aviary and thus were all familiar with each other. To determine the affiliative bonds within the group, twenty-minute videos were recorded at two different periods of time: (1) six videos between the 25th of April 2014 and 16th of May 2014 and (2) 21 videos between the 19th of December 2014 and the 2nd of February 2015. The first session of affiliative videos was recorded at the same time that the first two periods of food-sharing experiment and the second session of affiliative videos corresponded to the third period of food-sharing experiment. Behavioural observations were recorded on a camera (Sony Handycam HDR-CX410) fixed on a tripod (Vanguard Mak 203) using the “all occurrences and continuous sampling method”. Scored behaviours were the number of allopreening. Allopreening event was counted when a donor preened the receiver’s head or back. The allopreening stopped with the donor lifting its head. Videos were analysed using the software VLC media player, version 1.5.

Reciprocity and interchange

To investigate reciprocity and interchange, we used the program Matrix Tester (Hemelrijk, 1990a, 1990b) on Microsoft Excel to compute matrix comparisons, that avoided any biases linked to the dependency of data points. The TauKr statistic was calculated to obtain a correlation between cells of a same row in a matrix. Significance levels of the TauKr statistic were determined using a random permutation test (10 000 permutations). To investigate

reciprocity in food-sharing between individuals, the cofeeding (or stealing) matrix was correlated with its transposed version.

In order to investigate the occurrence of interchange, i.e. the exchange of food (either via stealing or via cofeeding) for another currency (affiliative behaviors such as allopreening), we run another serie of matrix analysis. To test interchange between cofeeding and allopreening, the actor matrix of cofeeding frequency (actor in rows) was correlated with the receiver matrix (receiver in rows) of allopreening frequency. We also did the same test with stealing instead of cofeeding. All periods of the food-sharing experiment were pooled for these matrix analyses. Because two birds did not participate in all testing periods, we computed the frequency of cofeeding and stealing for each donor-receiver dyad as proportion of the total trials in which each bird participated: 56 trials for birds that participated in all 4 testing periods, 42 trials for Viviane and 28 trials for Rama.

Also, the two observation periods in which affiliative interactions were recorded were pooled together for those matrix analyses. For the same reasons explained above, we computed allopreening as a proportion of the total observation duration (in minutes) for each donor-receiver dyad.

Statistical analysis

The main aim of our study was to test how the four possible feeding "strategies" (consuming, dropping, cofeeding, and stealing) developed over time and whether cofeeding and stealing was influenced by kinship and sex. We ran a generalized linear mixed model (GLMM) for each strategy. Models included the period of test (periods 1,2,3 or 4), the type of food exchanged (fennel or carrot), the relationship shared by the birds (siblings or non-kin) and the type of association formed by the birds (same-sex or different-sex pairs). For the consuming and dropping strategies, which involve only the donor bird, models also included individual

identity as a random effect. The cofeeding and stealing models included dyad identity as a random effect because two birds (donor and receiver) were involved. For any given strategy, the number of food pieces was pooled by period and by food type for each bird (consuming, dropping) or for each dyad of birds (cofeeding, stealing). A dyad was a unilateral relationship between two birds with one donor (the subject, i.e. the birds receiving the 10 food pieces consecutively) and one receiver. For the birds A and B, for example, two dyads were considered: the dyad A-B with A the donor and B the receiver; and the dyad B-A with B the donor and A the receiver. Moreover, only the dyads that exchanged at least one piece of food throughout the experiment (either via cofeeding or stealing) were included in the statistical analyses, resulting in 23 active dyads. A Gaussian distribution was used for the consuming and dropping strategies while a Poisson distribution was used for the cofeeding and stealing strategies. We checked for normality of residuals, normality of random effects and for overdispersion of the models. When a model was overdispersed, we corrected the standard errors by multiplying them by the square root of the dispersion parameter φ. Corrected p-values were then computed using the new standard errors (SE).

We also investigated how the number of recipients per donor evolved over time for the cofeeding and stealing strategies. We ran a GLMM for each strategy. Models included the testing period as a fixed effect and individual identity as a random effect. We used a Poisson distribution for both models and we checked for normality of residuals, normality of the random effect and for overdispersion of the model.

All statistical analyses were performed with R (R Development Core Team 2008) using the LME4 R package of Bates et al (2014) to run all models.

Study 2: Emotional response to conspecific distress calls in cockatiels

General experimental procedure

Each subject was tested three times, on three different days: one day with an artificial white noise, one day with a distress call from a partner (an affiliated individual) and one day with a distress call from a non-partner (sharing no affiliative bond). The conditions and the order of presentation of these three stimuli were semi-randomised and counterbalanced across the subjects (see Table 3). The experimental phase for each testing day took approximatively 30 minutes per bird. Each day of testing was separated by 4 to 5 days without experiment in order to minimize the stress of the separation from the other birds. The first seven birds were tested the 26th of November, the 1st of December and the 5th of December 2014 while the three last birds (Loki, Skadi and Odin) were tested the 22th, 27 and 31st of july 2015. Birds were tested alone, one at a time in sound proof chamber room to eliminate any possibility of being influenced by the presence of any other bird in the room. Behavioural responses of subjects were recorded with a webcam during the entire 30 minutes duration of the experiment.

Days of testing / Subjects	Day 1	Day 2	Day 3
Callisto	NP	WN	P
Hermès	WN	P	NP
Nephtys	P	NP	WN
Seth	WN	P	NP
Sita	P	NP	WN
Viviane	WN	P	NP
Wala	NP	WN	P
Loki	NP	WN	P
Odin	P	NP	WN
Skadi	WN	P	NP

Table 3. Randomization of conditions depending on the subjects and the days of testing. P: Partner, NP: Non-partner, WN: White Noise.

Degree of affiliation

All birds were group-housed in the same aviary and thus were all familiar with each other. In order to create experimental dyads of partners and non-partners for each test bird, we determined the strongest and weakest affiliative relationship of each cockatiel in the group. Affiliative relationships were assessed via affiliation indexes based on socio-positive behaviors. Partners exhibited a high index (422.18 on average; minimum: 58.92; maximum: 930.74) and non-partners alow inde of association (1.66 on average, minimum: 0; maximum: 4.71, see Table 4 and 5). The difference in the indexes of affiliation between partner and non-

partner was at least 45.0. Each bird was tested with a partner and a non-partner of the same sex. For example, if a female was tested with another female as a partner, the non-partner was also a female. Because of the bias in sex ratio between subgroups (there was only one female, Nephtys, in the "siblings" subgroup and only one male, Hermès, in the first unrelated subgroup, calls of these individuals were used several times as non-partners stimuli.

Subjects (sex)	**Age (years)**	**Partner (sex)**	**Relation with the subject**	**Age (years)**	**Index of affiliation Subject/Partner**	**Non-Partner (sex)**	**Age (years)**	**Index of affiliation Subject/Non-Partner**
Seth (M)	1,5	**Nephtys (F)**	Siblings	1,5	930.74	**Wala (F)**	1,5	0.42
Hermès (M)	1,5	**Viviane (F)**	Mated pair	1,5	648.66	**Nephtys (F)**	1,5	4.71
Odin (M)	1	**Skadi (F)**	Mated pair	1	103.13	**Callisto (F)**	1,5	2.29
Loki (M)	1	**Viviane (F)**	Heterosexual pair	1,5	48.92	**Sita (F)**	1,5	0
Nephtys (F)	1,5	**Seth (M)**	Siblings	1,5	930.74	**Hermès (M)**	1,5	4.71
Viviane (F)	1,5	**Hermès (M)**	Mated pair	1,5	648.66	**Seth (M)**	1,5	2.08
Sita (F)	1,5	**Wala (F)**	Same-sex pair	1,5	231.05	**Nephtys (F)**	1,5	0
Wala (F)	1,5	**Callisto (F)**	Same-sex pair	1,5	457.10	**Nephtys (F)**	1,5	1.52
Callisto (F)	1,5	**Sita (F)**	Same-sex pair	1,5	119.75	**Nephtys (F)**	1,5	0.42
Skadi (F)	1	**Odin (M)**	Mated pair	1	103.13	**Seth (M)**	1,5	0

Table 4. **Characteristics of the subjects, partners and non-partners**: gender (F: Female; M: Male), age (in years), relationship between the subject and the partner, index of affiliation shared with the partner and non-partner

Emitter / Subject	Callisto (F)	Hermès (M)	Nephtys (F)	Seth (M)	Sita (F)	Viviane (F)	Wala (F)	Loki (M)	Odin (M)	Skadi (F)
Callisto (F)	/	0.28	**0.42**	0	**119.75**	0	457.10	0	2.29	3.93
Hermès (M)	0.28	/	**4.71**	1.80	115.50	**648.66**	29.21	0	0	0
Nephtys (F)	0.42	**4.71**	/	**930.74**	0	4.15	1.52	0	0.41	0
Seth (M)	0	1.80	**930.74**	/	5.95	2.08	**0.42**	0.37	1.19	0
Sita (F)	119.75	115.50	**0**	5.95	/	99.22	**231.05**	0	0	53.06
Viviane (F)	0	**648.66**	4.15	**2.08**	99.22	/	8.44	48.92	5.67	0
Wala(F)	**457.10**	29.21	**1.52**	0.42	231.05	8.44	/	19.10	28.89	6.58
Loki (M)	0	0	0	0.37	**0**	**48.92**	19.10	/	3.43	35.29
Odin (M)	**2.29**	0	0.41	1.19	0	5.67	28.89	3.43	/	**103.13**
Skadi (F)	3.93	0	0	**0**	53.06	0	6.58	35.29	**103.13**	/

Table 5. Affiliative indexes of all possible dyads of birds used to create experimental dyads for the playback experiment. Each subject heard the calls of a preferred partner (index in bold red letters) and calls of a non-partner (index in bold black letters).

In order to monitor the affiliative interaction within the group, twenty-minutes videos were recorded at three different period of time: 1) six videos in May 2014, six months before the present study in order to assess the general dynamics of relationships between the 7 first birds in order to determine the experimental dyads for the seven birds; 2) 21 videos in December 2014 and January 2015, just after testing the first seven birds, in order to revalidate the choice of the experimental dyads and 3) 18 videos in April 2015, before testing the last three birds (Loki, Odin and Skadi) to create the experimental dyads for these individuals, which had been integrated into the group at a later point in time. In order to determine the affiliative bonds within the group, we created an index of affiliation (see further below). The index of

affiliation was based on the data collected during the last two sessions, because they reflected the dynamics of relationships between birds at the time of the playback experiments. Indeed, we observed that some affiliations, especially between males, observed in the first session of videos no longer existed in the second session for the seven birds. Behavioural observations were recorded on a camera (Sony Handycam HDR-CX410) fixed on a tripod (Vanguard Mak 203) using the "all occurrences and continuous sampling method"(Altmann, 1974). Videos were analysed using the software VLC media player, version 1.5.

For each dyad, we constructed an index of affiliation following Silk et al.'s procedure (2006) which was adapted to birds by Boucherie et al. 2016. Recorded behaviours were: the time (in seconds) spent in spatial proximity (PROX, i.e. the distance between two birds was so small that they could touch each other), and affiliations, which included the frequency of solicitation of allopreening (SOL) and the frequency of allopreening (ALO) during the interval of observation. Allopreening is the equivalent of allogrooming in primates. It was counted when a donor preened the receiver's head or back and stopped with the donor lifting its head. A solicitation for allopreening is an easily recognized ritualized posture where one individual bows its neck presenting it to its partner. A sollicitation was scored when the begging partner lifted its head. We created the index as follow:

$$S_{hv} = \frac{((PROX_{hv}/PROX) + (ALO_{hv}/ALO) + (SOL_{hv}/SOL)) \times 100}{3}$$

With S_{hv}, the index of affiliation of the hv dyad (i.e. the dyad constituted of the subject named h and its partner named v); $PROX_{hv}$ the dyadic frequency of spatial proximity for the hv dyad, divided by PROX which equals to the overall mean frequency for all possible dyads (and similarly for the other variables: ALO and SOL). The denominator is fixed and refers to the

number of variables. The value of the index of affiliation increases with the strength of a relationship.

To reduce any biases due to the specificity of single calls, we played back as many different distress calls (from different emitters) as possible. For the partner playback stimulus, we chose dyads with the highest indexes of affiliation except in the case of Callisto, since we wanted to use as many different calls as possible. We then broadcasted Sita's calls to avoid using Wala's calls twice. Consequently Callisto was paired with a partner with a high index of affiliation (Sita) but not the highest possible one (Wala). To reduce any effect of the emitter's sex rather than degree of affiliation on the subject's behaviour, each subject was presented with the distress call emitted by two birds (partner and non-partner) of the same sex and of comparable age

Distress calls recording procedure

We created playback sequences of distress calls of each bird. These calls were obtained from recordings of a stressful event. For this purpose each bird was individually isolated in a cage (41 cm x 24 cm x 29.5 cm) placed in a sound proof chamber away from the aviary. An unfamiliar experimenter (-so as to avoid fear reactions towards their usual experimenter-), then briefly (for ca. one minute) inserted his hand in the cage wearing a large leather glove. The same leather gloves were used when the birds were handled for medical care and were therefore associated by the birds with being seized. Consequently, birds usually started to emit alarm calls when they saw the glove. When the gloved hand reached into the cage, the birds emitted distress calls, which are specific calls produced when the animal is physically

restrained. These distress calls are characterized by repeated harmonic harsh high-pitched calls (see Figure 7 for an exemplary spectrogram).

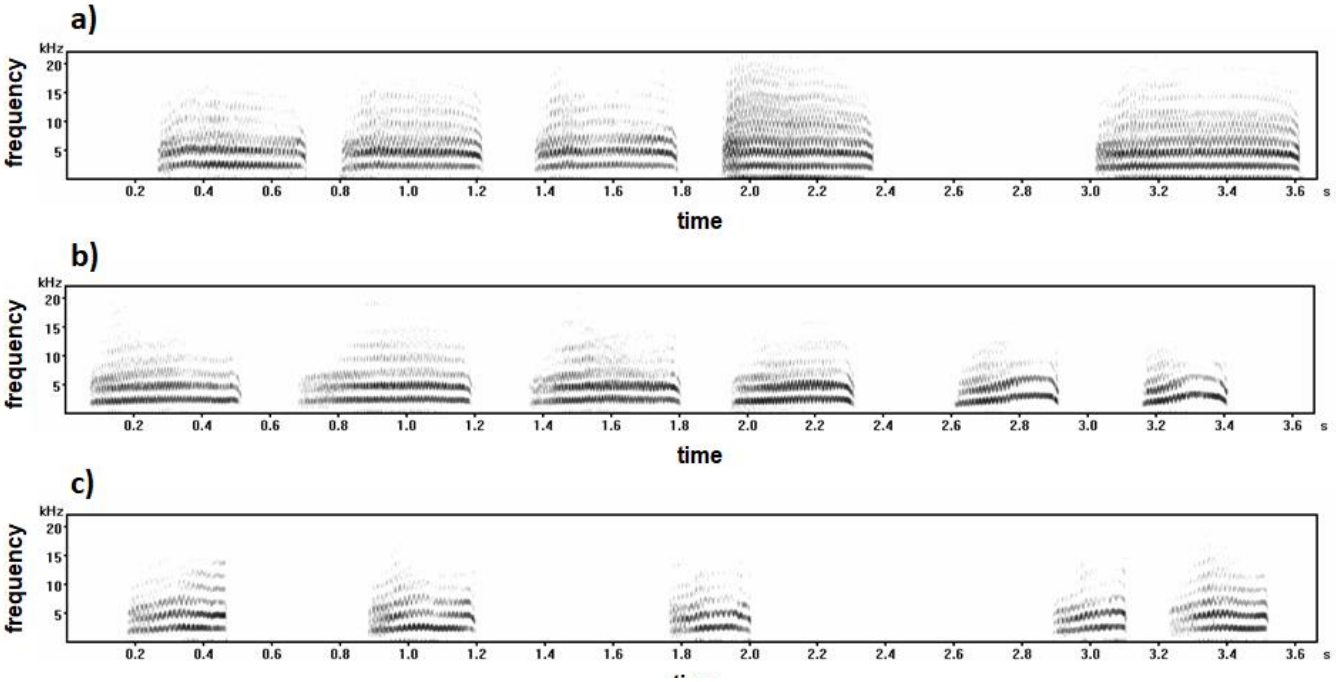

Figure 7. Spectrogram displaying the first calls from (a) Wala, (b) Sita and (c) Hermès extracted from the distress call sequences used in the experiment. Each playback stimulus was constituted of 10 different calls from the same bird, which were repeated 3 or 4 times to obtain 30 seconds of playback for each emitter.

Calls were recorded throughout one minute per bird approximatively. The vocalizations of the subjects were recorded with a Sennheiser microphone (MD21U) set up in its stand (Sennheiser MZT 100) and a Marantz recorder (Marantz PMD 670; sampling rate: 44100 Hz; accuracy: 16 bits, mono) and were collected in WAV format. Each bird was released back to the aviary immediately after the recording session. One bird never emitted distress calls (Loki) and consequently he could only be tested as subject. Two recording sessions were conducted, one in October 2014 with seven birds, and another one in June 2015, in order to record the calls of the three birds that were integrated into the group later and therefore had not been recorded during the first session (Loki, Skadi and Odin).

Preparation of the playback stimuli

Two types of stimuli were created: distress calls and artificial white noise. Both stimuli were computer-edited using Avisoft SASLab Pro, version 5.0.14 (Raimund Specht, Berlin, Germany).

In order to create comparable distress call stimuli from each individual, we selected 10 different calls per stimulus per bird and individually normalized them to 75% with an automatic feature in Avisoft SASLab Pro software, which adjusts the intensity of the different calls. The 10 different calls per bird kept for creating the stimulus were chosen for being distinctly audible, with no sound saturation or parasite sounds. All calls were clipped from the original recordings which were recorded on the same day. Consequently, all playback stimuli were comparable in intensity. When possible, we kept consecutive suitable calls (with no saturation or background noises) in the same order and with the original silent intervals between them. The goal was to keep the final playback sequence as close to the original distress calls as possible. Where we could not obtain 10 calls per stimulus in a natural sequence, we added in calls clipped out randomly from the recordings and placed short silent intervals of different durations (usually less than 1 second) in between. We obtained in the end 10 calls per stimulus per bird.

In order to get a final duration of 30 seconds per playback stimulus, we repeated the 10 calls several times. We usually had 4 repetitions of 10 calls per 30 seconds of playback stimulus (with the exception of Seth and Viviane who emitted very long calls and consequently only 3 repetitions of 10 calls per 30 seconds were played back for these birds). The segmentation of each call was achieved with outline syllables parameters on Sound Analysis Pro 2011 software (Frequency range: 22050 Hz, FFT data: 10 ms, Advance window: 1.5 ms, contour tresh: 10). The final single distress calls exhibited the following characteristics (±SE): mean

duration of 502 ± 61 ms (range: 296-869, n=9); mean fundamental frequency of 2135 ± 114 Hz (range = 1677- 2543, n =9), mean frequency of 3478 ± 181 Hz (range: 2874-4428, n=9). The broad-band white noise playback stimulus was a continuous audio stimulation lasting 30 seconds with no silence parts inserted and automatically generated with a feature in Avisoft SASLab Pro software (0 - 22050 Hz). White noise serves as a good control as it can trigger an important level of attentional state but is free of any emotional value. These findings has been reported by a study on pigs (Düpjan et al., 2011), in which the pigs' behaviours did not differ between playback of conspecifics versus white noise control sounds

Each stimulus was played back at the same amplitude, with a maximum noise level of 91 dB (re. 20 μPa ; measured with a Ro-LINE SPL meter 1, using 'A' weighting at the typical position of the test bird), 15 cm from the loudspeaker, which reflects natural amplitude levels.

Experiment procedure of the playback

Each test comprised three distinctive phases: “before”, “during” and “after” playback stimulus (Figure 8). It began with a 10 minutes phase of silence referred to as “before”, which preceded the first playback stimulus. This silence phase was necessary for allowing the bird to calm down after being removed from the aviary and habituate tothe cage in the sound proof chamber. Then, a 30 seconds audio stimulus was played back. This phase we refer to as “during” since it constitutedthe actual playback audio stimulus. Three replications of the same audio stimulus (either distress call or white noise) of 30 seconds were played back, with a 5 minutes interval of silence in between the different playback stimuli. These 5-minutes silence phases following each playback stimulus were called “after” and occurred three times in total per test

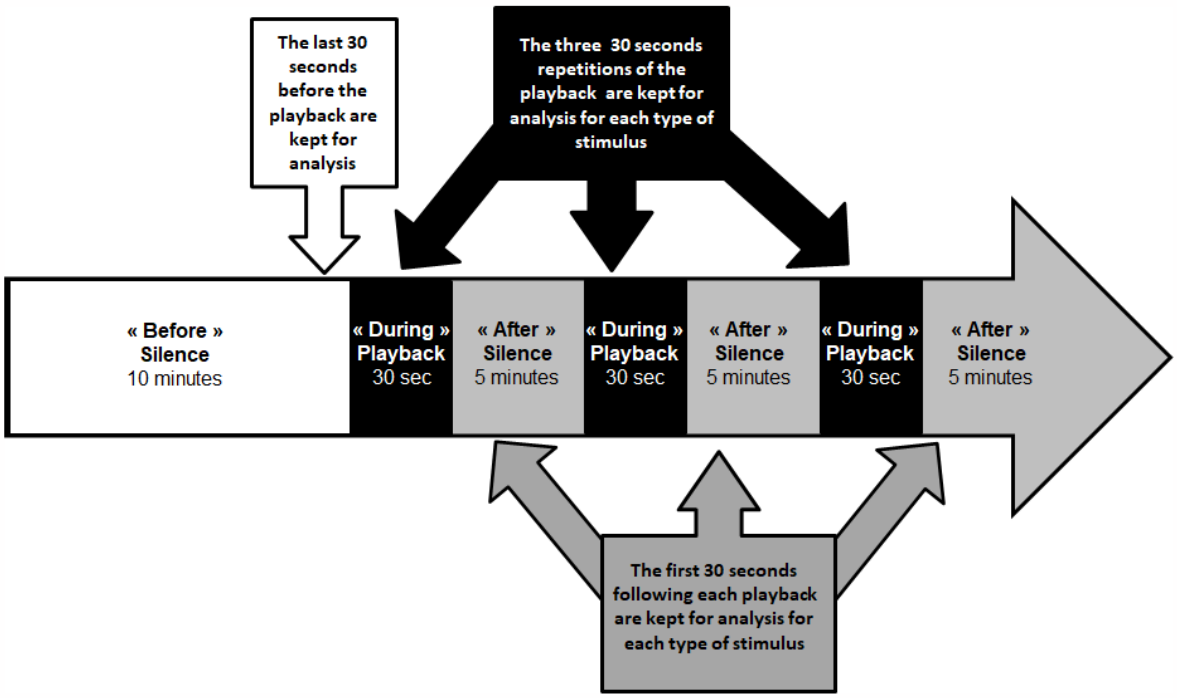

Figure 8. **Schematic representation of the playback sequence**. Three distinctive phases are represented: the 10 minutes silent phase before the playback stimulus (“Before” in white), the three 30 seconds repetitions of the playback stimulus (“During” in black) and the 5 minutes silent phases following each playback stimulus (“After” in grey). The arrows show the exact parts kept for analysis: the 30 last seconds of the “Before” phase, each repetition of 30 seconds of each stimulus in the “During” phase and the first 30 seconds of each “After” phase.

Each bird was tested alone: animals were individually caught in the aviary, then put in a cage (41 cm x 24 cm x 29.5 cm) and placed in the sound proof chamber (69 cm x 49.5 cmx 49.5 cm) via a two- way casement window on the left of the sound proof chamber on the figure (Figure 9). On the right, the sound-proof chamber was put near a wall. The experimenter left the room after closing the window and starting the broadcast of the stimulus. Consequently, birds were left alone during the all experiment and could not see anything outside of the sound-proof chamber. The surroundings of the cage inside the sound-proof chamber were constituted of a microphone, the loudspeaker and the webcam, hung on the ceiling of the sound-proof chamber

A cup filled with 10 grams of millet was placed in the middle of the cage. Three lines were drawn on the Kraft paper inserted in the bottom of the cage to create three distinctive zones (13.5 cm long for each zone) (Figure 9). The first zone was the closest sector around the loudspeaker, the second zone was the middle one into which the cup with the 10 grams of millet was placed, and the third one was the most distant zone from the loudspeaker.

The behaviour of the birds was recorded using a webcam (Logitech HD Pro C920) connected to a computer (HP Pavillon dv6000). A Sennheiser microphone (MD21U) with its stand (Sennheiser MZT 100) was used to record calls emitted by the subject on a Marantz PMD 670 recorder. We played back both distress calls and white noise stimuli from the same 60 Watts Mini Elipson Horus loudspeaker (frequency response: 80 Hz - 20 kHz) placed in the back of the sound proof chamber at 15 cm distance from the cage. The loudspeaker was connected to a stereo amplifier Pioneer A-209R linked to a second Marantz PMD670 digital recorder (bandwidth: 20 Hz - 20 kHz ± 1dB).

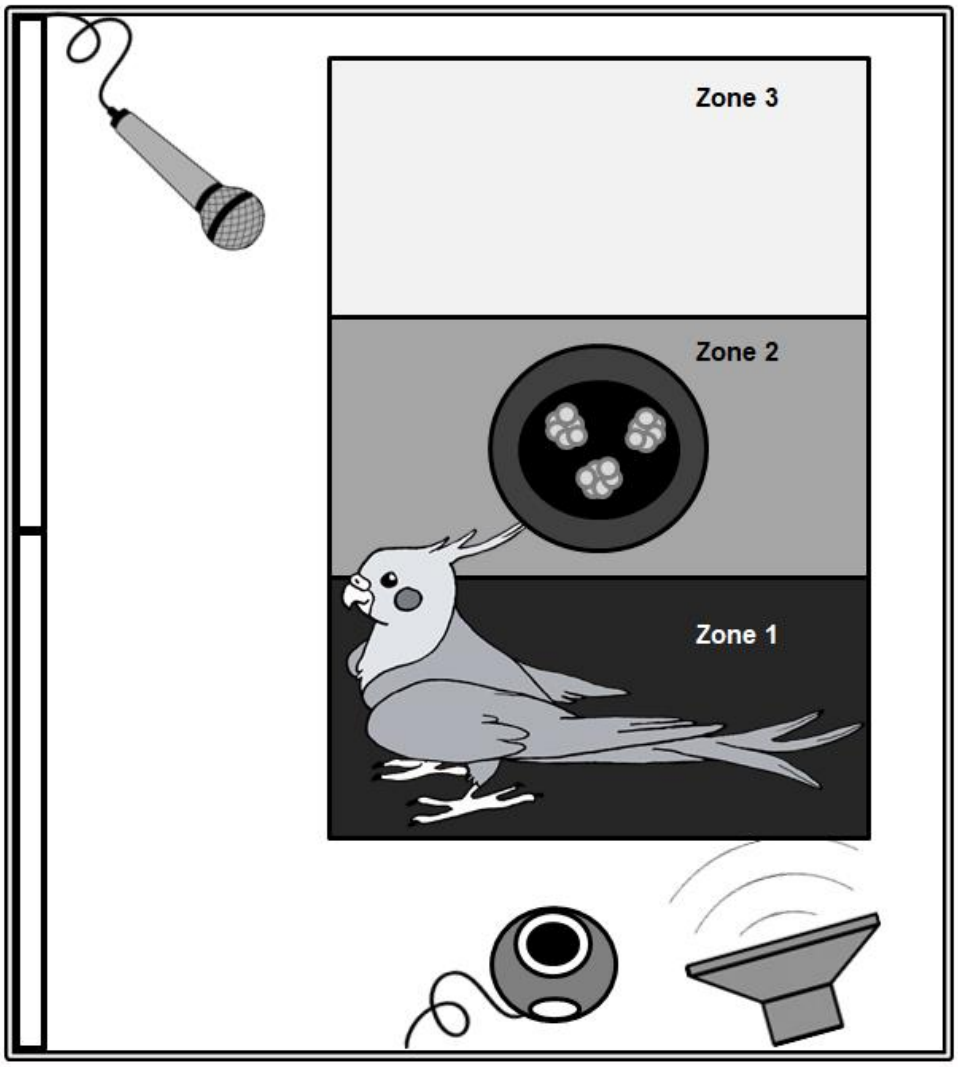

Figure 9. **Experimental apparatus (Top view)**. The bird is placed inside a sound proof chamber in a cage separated in three distinctive zones (zone 1 near the loudspeaker, zone 2 with a cup filled with millet, and zone 3 the furthest from the loudspeaker). The entrance of the sound-proof chamber is on the left via a two-way casement window. A webcam and a loudspeaker are positioned near the cage and a microphone recorded the subject's calls.

Behavioural analysis

The videos of the birds' behavioural responses were coded with a time-precision of one-tenth of a second while using the Solomon Coder Beta software, version 15.01.15 (Copyright András Péter, http://solomoncoder.com). The birds' behaviours were analysed during the three phases of the experiment: the 30 seconds of silence before the first playback stimulus ("before"), the three playback stimulations of 30 seconds each ("during") and the 30 seconds of silence following each playback stimulus ("after").

The following variables were coded: activity (the number of changes from one zone to another), number of calls emitted by the subject, time spent near the loudspeaker (designated as zone 1), and time spent with crest 1 position (Figure 10). All these variables measured stress and alertness (for crest 1 position).

Locomotion represented by the changes from one zone to another and the avoidance of the zone close to the loudspeaker are usually used to assess the emotional arousal of animals and their motivation to flight. If the bird is stressed, we expect it to move around more nervously in the cage and therefore cross the zones more frequently. Vocalizations are known to reflect emotional states in humans and non-human mammals (Briefer, 2012). For example, in piglets, scream rate increased when aroused (Linhart et al., 2015). Our cockatiels emitted high pitched calls, which are alarm calls characteristically given in the presence of predators or other sources of danger (Gill & Bierema, 2013) The last variable, the crest position is known to express emotional states in birds an can be expressed in several context like fear or fights.

Three different crest positions were distinguished: “Crest 1” corresponded to a crest totally erected i.e in vertical position on the forehead, which occurs when the bird is highly aroused, attentive and/or stressed, “Crest 2” was the intermediate position and “Crest 3” corresponded to the crest of a relaxed bird, laid flat on the head. However, in the analysis we focussed on crest position 1 solely, because it was the clearest indicator of stressand therefore we only integrate this variable in the model, to avoid redundant results.

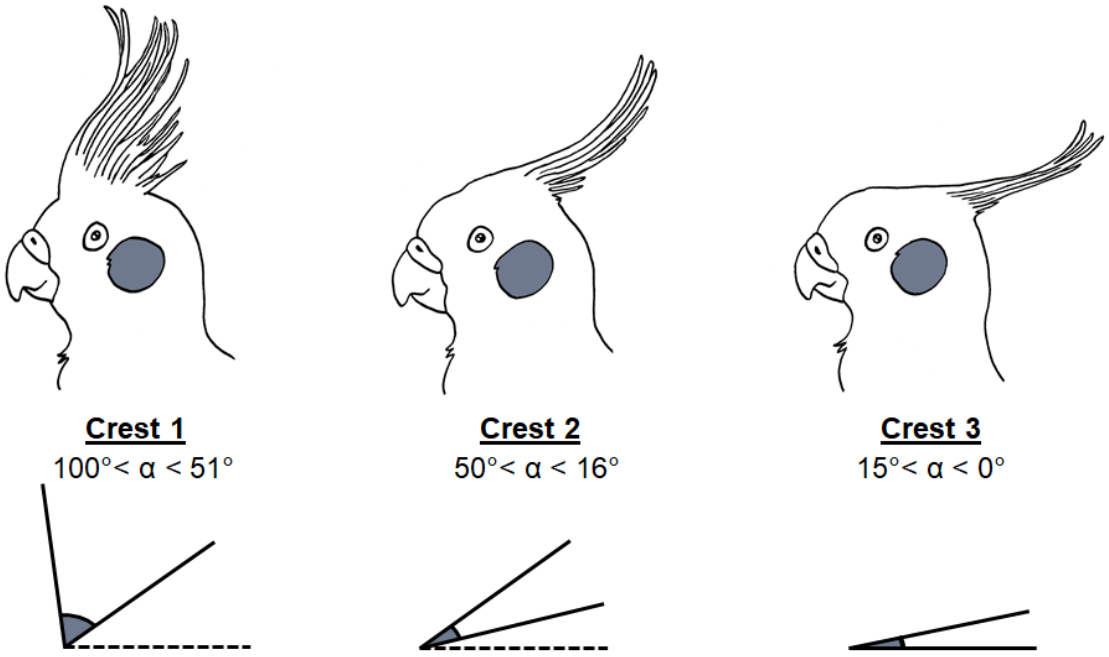

Figure 10. **Schematic representation of the crest positions**. Crest 1 position is characteristic of a stressed or attentive bird, with clearly separated feathers. The second position is intermediate and the Crest 3 position is observed in entirely relaxed birds e.g. while resting.

Statistical analysis

Our first objective was to test whether the birds reacted more during the playback stimuli than before and after stimulation. We ran a generalized linear mixed model (GLMM) for each of our four response variables: activity (the number of zone changes), number of calls emitted by the subject, time spent near the loudspeaker (designated as zone 1), and time spent with crest 1 position. Models included the type of playback stimulus (partner, non-partner and white noise), the phase (before, during and after the playback stimuli) and the sex of the subject as fixed effects. Models also included individual identity, day of testing and the interaction between days of testing and order of stimulations as random effects.

The second objective was to investigate whether birds reacted more to distress calls than to white noise and whether they responded more strongly to partner calls than to non-partner calls during the playback stimuli. For this, we ran a second set of GLMMs only using the data

from the “during” phases. The models included the type of playback stimulus (partner, non-partner, white noise) and the sex of the subject as fixed effects. Again, interactions could not be tested because the models did not converge. The models also included individual identity, the days of testing and the interaction between days of testing and order of stimulations as random effects.

Finally, we created another set of GLMMs to investigate the birds’ behavioural responses after the end of the stimuli, i.e. during the “after” phases. We wanted to check if the type of stimulus had an impact on the birds’ behaviours after the end of the audio stimulation. The third set of GLMMs was identical to the second set.

The activity and number of calls variables followed a Poisson distribution. Since the time spent near the loudspeaker and the time spent in crest position 1 variables were binomially distributed, we transformed them in binary variables and used a binomial distribution. The time spent near the loudspeaker variable was categorized as spending less than or at least 10 seconds out of the 30 seconds of each playback stimulus near the loudspeaker, and the time spent in crest 1 position variable was categorized as spending less than or at least 25 seconds out of 30 seconds playback stimulus in crest 1 position. The cut was defined by means of the breaks in the histograms. Results for these two behaviors are shown as percentage of audio stimulations for which the subject exhibited either a crest 1 for more than 25 seconds or spent more than 10 seconds near the loudspeaker. We checked for normality of random effects and for overdispersion of the models. When the models were overdispersed, we corrected the standard errors by multiplying them by the square root of the dispersion parameter φ. Corrected p-values were then computed using the new standard errors (SE).

All statistical analyses were performed with R (R Development Core Team 2008) using the LME4 R package of Bates et al. (2014) to run all models.

Study 3: Testing prosociality in an experimental task with psittacids

Experiment 1: Other-regarding preferences in psittacids

Materials

Three different items per bird per set were used across this experiment and this experiment is run three times, each time with a new set of objects. Several objects of different sizes and colors, like plastic screw bottle caps, plastic bottle rings, pens, pen caps (depending on the replication) were used with African grey parrots, and plastic screw bottle caps and carabiners were used with the other species (see Supplementary Methods). We used three different sets of objects to avoid any preference bias and assess the ability of birds to understand the value of tokens for each set.

For African grey parrots, the items were presented in front of the subject on a table (120 x 60 x 75 cm) inside the aviary. The experimenter sat in front of the subject with the palm of his hand up in order to receive the item the bird chose. The receiver was perched, 50 cm away from the subject, but could not directly interact with the items on the table. The choice of the parrot was validated when the bird took the item and put it in the experimenter's palm (see Figure 11a).

For other parrots the experiment has been realised through the wire mesh of their aviaries in the indoor part (2 x 2 x 2 m) because they were less tamed. Two options have been used to display an object: either items were placed on a table in front of the subject or carabiners (used in another repetition of the experiment) were attached to the wire mesh, side by side, in front of the subject. The choice of a bird was validated when the bird touched the object with its beak. The partner could not interact with the items directly either (see Figure 11b).

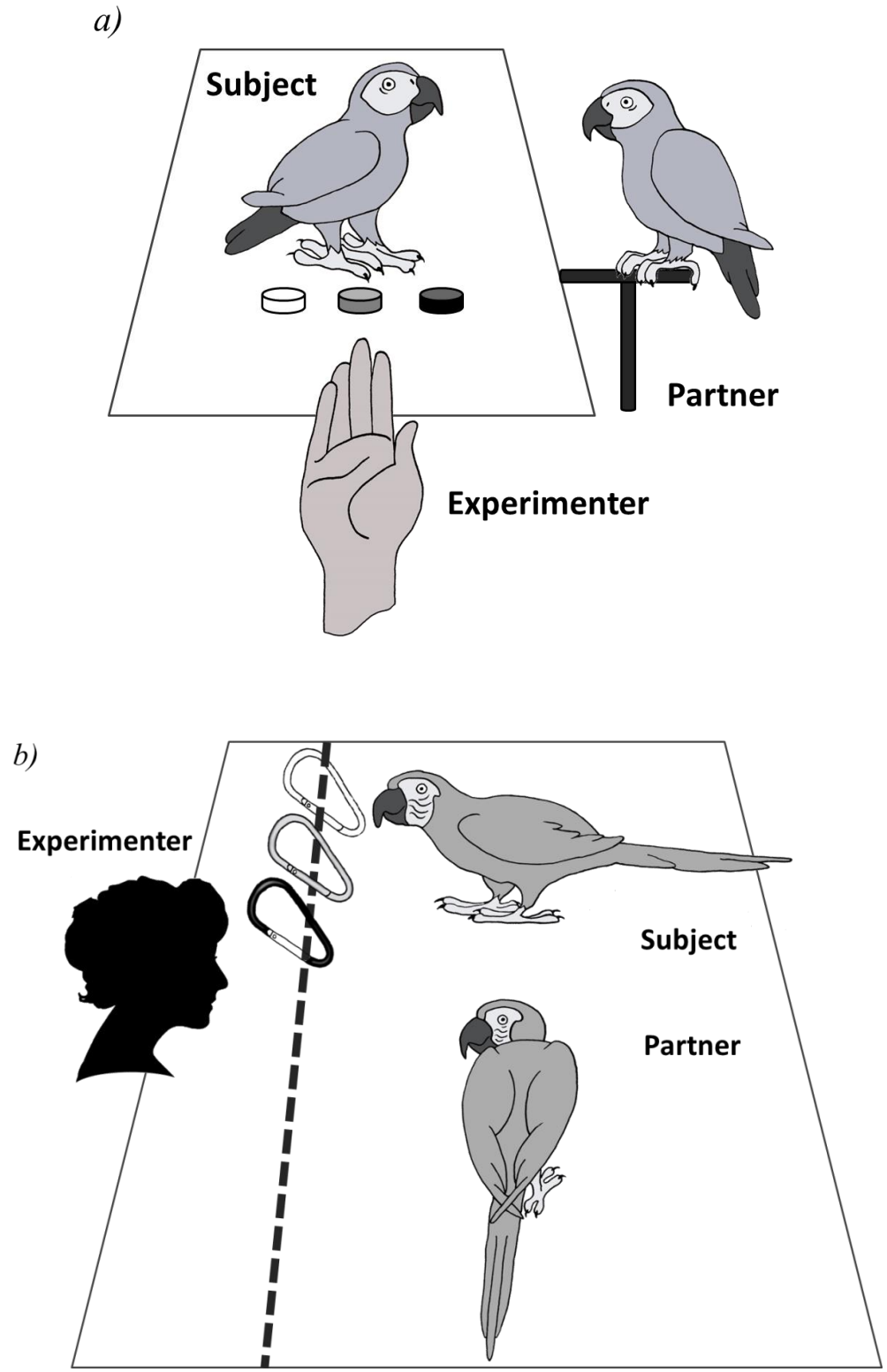

Figure 11. (a) Experimental set-up for experiment 1 as used with African grey parrots inside the aviary. The subject had to choose one item and to put it in the experimenter's hand. Birds received rewards depending on the item chosen. (b) Experimental set-up for experiment 1 as used with macaws and conures. The subject had to touch the chosen item with its beak. Birds received rewards depending on the item chosen.

Procedure

The Prosocial Choice Task (PCT) paradigm was used for the three experiments described in this paper. Birds had to choose one object among a set of three items to receive the associated reward. When chosen, the "no reward" item gave no access to the reward for any bird. When the subject chose the "own reward" item, he was the only bird to be rewarded. And when the subject chose the "both reward" option, the prosocial alternative, both birds obtained a reward. In this case, the partner received a reward a few seconds before the subject in order to help the subject to understand the outcome of this item. The latency to obtain a reward for the subject is kept still really short (less than 5 seconds) to prevent a time-based preference for the "own reward" object in the subject. When the subject chose the "no reward" object, the experimenter removed the objects and stopped interacting during six seconds. Except for giving zero, one or two rewards, the experimenter's behaviour did not differ no matter what the subject chose. When the bird chose one of the two other objects, the experimenter removed the objects while he gave the reward to the birds. It prevented the subject to choose two items in a row. The next trial started after a time out or when the parrots stopped eating. African grey parrots received sunflower seeds as rewards whereas macaws and conures received peanuts. The rewards were not visible during the experiment and were only delivered after the choice.

The experimental period for each set of objects with each group of birds (African grey parrots on one hand, other parrots on the other hand) lasted about one month. One month of non-testing period was included between each set.

Familiarization

Birds had the opportunity to interact with the objects before starting the test phase of the experiment. Each bird was offered 10 choices and if any object was chosen eight times or more out of 10 it would be replaced by another object. That way, we ensured that some colours, shapes or patterns were not preferred over others. The birds then learned to touch (for the macaws and conures) or bring back the object in the experimenter's hand palm (grey parrots) to receive a reward with an item different from the objects used in the test phase.

Test

Birds were tested in dyads but only the subject could approach and manipulate the objects. Each session consisted of ten trials per bird and lasted between 15 and 30 minutes depending on the bird's motivation. Roles were exchanged at the end of each 10 trials. Twenty sessions of 10 trials with each dyad were performed. The ten first sessions are necessary for the bird to understand the value of each object. The success criterion was reached when a bird did not choose the "no reward item" more than two times out of 10 trials in three successive sessions (30 trials). If the bird did not reach the success criterion at the end of the ten first sessions, ten more sessions of training were added. Only the last ten sessions were kept for analysis. Hundred trials were kept for analysis per set per bird, which means that 300 trials were analysed per bird in total, for the whole experiment.

All items were presented side-by-side in a counterbalanced order for each possible choice and the birds could interact freely with them. Each individual was tested with three different sets of objects and we changed the set across the replications in order to point out any stable preference.

We recorded the items chosen by the subject, but also the birds vocalizations and behaviours, usually linked to frustration such as cardboard biting, beak scraping and frustration calls. We

also recorded the reward anticipation when the partner approached the experimenter as soon as the subject touched the prosocial object.

Statistical analysis

Only the 10 last sessions for each set were kept for analysis. We ran normality test (Shapiro-Wilk test) and equal variance test (Levene test) before each analysis.

Two-way RM Anovas were used to compare birds' choices (African grey parrots on one hand, other parrots on the other hand) with all individuals pooled together and were followed by a Holm-Sidak post-hoc test for pairwise comparisons. A One-way RM Anova followed by a Holm-Sidak post-hoc test was conducted to compare anticipation events in partners depending on the item chosen by the subject. Friedman Repeated Measures (RM) Anovas on ranks followed by a post hoc Tukey test were used to test for differences in object selection at the individual level. All analysis were done with Sigmaplot® v.12 software.

Experiment 2: Influence of inequity on other regarding-preferences

Material

We used the same PCT paradigm in the same setting as in the first experiment: each subject had to choose between three different items associated with several different reward values: "no reward", "own reward" and "both reward". We used the same set of objects used during the third repetition of experience 1 (see Supplementary Methods).

Procedure

Food preference test were conducted to assess birds's preferences for food items. They had the possibility to choose between different food items. The preferred food was parrot formula (Nutribird 21) for Zoé and Léo and sprouted sunflower seeds for Shango. The low value

reward was dry sunflower seeds for all birds. Except for the rewards received, the procedure was the same as in the first experiment.

In this experiment, two conditions were tested with different consequences for the choice of the "both reward" item. In half of the trials, in the control condition, both birds received the same amount of the less preferred food when the subject chose the "both reward" item. In the other half of trials, the other condition was the inequity condition: the partner received a better treat than the subject, when the latter chose the "both reward" item. The conditions were alternated across the sessions. All items were presented side-by-side, in a counterbalanced order for each possible choice and the subject could interact freely with them.

Eight sessions of 10 trials were conducted for each condition (control and inequity conditions), so 160 trials per bird in a whole. Fewer sessions than in experiment 1 have been needed, since the birds were already trained with these items.

We recorded the items chosen by the subject, but also the birds vocalizations and behaviours, usually linked to frustration such as cardboard biting, beak scraping and frustration calls.

Statistical analysis

We ran normality test (Shapiro-Wilk test) and equal variance test (Levene test) before each analysis. Two-way RM Anovas were used to compare birds' choices with all individuals pooled together and were followed by a Holm-Sidak post-hoc test for pairwise comparisons. Friedman Repeated Measures (RM) Anovas on ranks followed by a post hoc Tukey test were used to test for differences in object selection at the individual level. All analysis were done with Sigmaplot® v.12 software.

Experiment 3: Influence of other regarding preferences on the maintenance of cooperative behaviour

Material

The birds were tested on a table (120 x 60 x 75 cm) where two different areas were delimited using a screen constituted by a piece of cardboard (65 x 0.6 x 12.5 cm) fixed on a wooden base (55.5 x 6.5 x 1.5 cm) The parrots could see each other and have physical contact over the cardboard but, only the subject (Léo) could choose one of the items. Objects were placed on the table in front of Léo who had to choose one object and give it to the receiver (Shango) over the cardboard screen (see Figure 12). The set of three items used during the test phase was the same than the one used with Léo during the first repetition of the first experiment: plastic bottle screw caps of different colors (see Supplementary Materials). Since birds already succeeded to attribute rewards to items during the different replications of experiment 1 and 2, we chose a set already used one year before in order to shorten the familiarization phase.

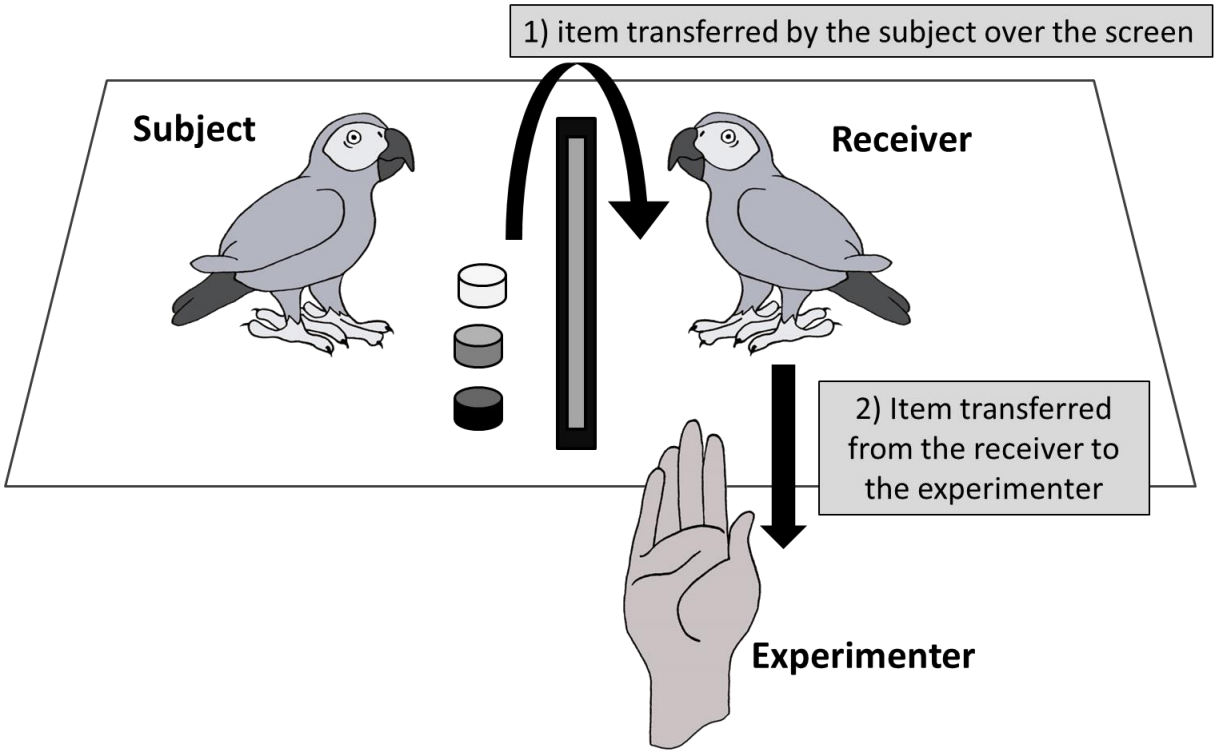

Figure 12. Experimental set-up for experiment 3. The subject chose one item and then, had to cooperate with the receiver via two successive actions in order to obtain a reward depending on the chosen item. Léo transferred the item over the screen to Shango who had to give the received item in the experimenter's hand in order to obtain a reward.

Procedure

We used the same PCT paradigm as in the first two experiments but we introduced cooperation in it. In this experiment, Léo had to choose between three different items associated with several different reward values: "no reward", "own reward" and "both reward" and had to give it to Shango, who was waiting on another side of a cardboard screen. Then, Shango had to put the item in the experimenter's hand palm in order to be rewarded, depending of the item's value he received. Birds were rewarded only if the item was given to the experimenter. If Shango refused to collaborate and to bring the item to the experimenter, no birds were rewarded at all.

Familiarization

The birds had to be habituated at staying close to the cardboard screen separating the two parts of the testing area. They also had to be habituated to stay on the table and to manipulate the objects in their own testing area without crossing the cardboard screen.

The birds were first familiarised for two weeks with the transfer of an item over the screen. This item was different from the objects used during the earlier experiments (a new bottle cap the two parrots never saw before). Thirteen days of training with two sessions of 30 minutes each morning, and two sessions of 30 minutes each afternoon were needed for the two birds to learn the succession of actions required to obtain the reward. The success criterion was passed when a bird did not choose the "no reward item" more than two times out of 10 trials during three successive sessions.

Test

The three items were placed on the table in front of Léo, and close to the screen, separating him from Shango. All items were presented side-by-side, in a counterbalanced order for each possible choice and Léo could interact freely with them. The rewards were not visible during the experiment and were only delivered after the choice.

Twenty-two sessions of 10 trials were conducted during this experiment. Each session lasted approximatively 30 minutes but could be shortened, depending on the birds' motivation

We recorded the items chosen by Léo, the items transferred by Shango (we recorded a success if Shango gave the item to the experimenter and a fail if he did not) but also Shango's vocalizations and behaviours, usually linked to frustration.

Statistical analysis

We ran normality test (Shapiro-Wilk test) and equal variance test (Levene test) before each analysis. Friedman Repeated Measures (RM) Anovas on ranks followed by a post hoc Tukey test were used to test for differences in Léo's choices. Fisher's exact tests were used to test for differences in Shango's transfers but also other behaviors he expressed depending on the item he received from Léo such as frustration (cardboard biting, beak scraping and frustration calls), throwing away the item, and flying away from the apparatus during the test. Fisher's exact tests were done. The evolution of Shango's actions across the sessions was assessed while running a Spearman rank order correlation. All analysis were realized with Sigmaplot® v.12 software, except for the Fisher exact tests done with R software (v.3.3.2).

Supplementary methods

Figure 13. Experiment 1_set 1 (African grey parrots)

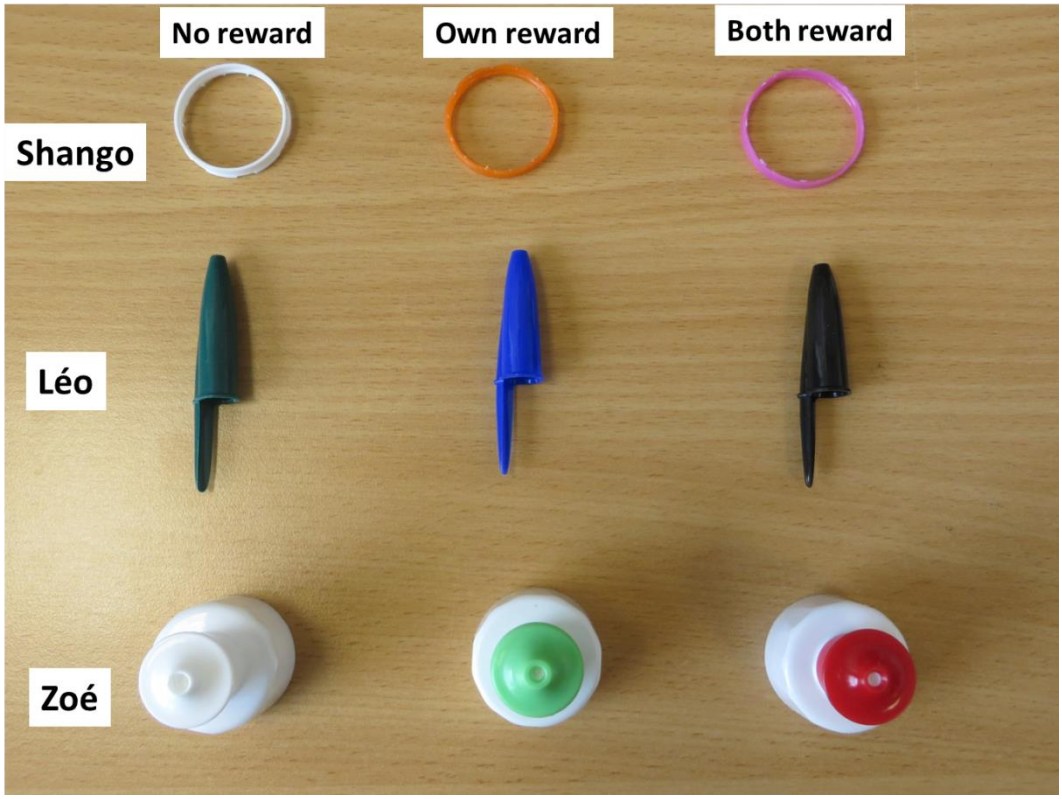

Figure 14. Experiment1_set 2 (African grey parrots)

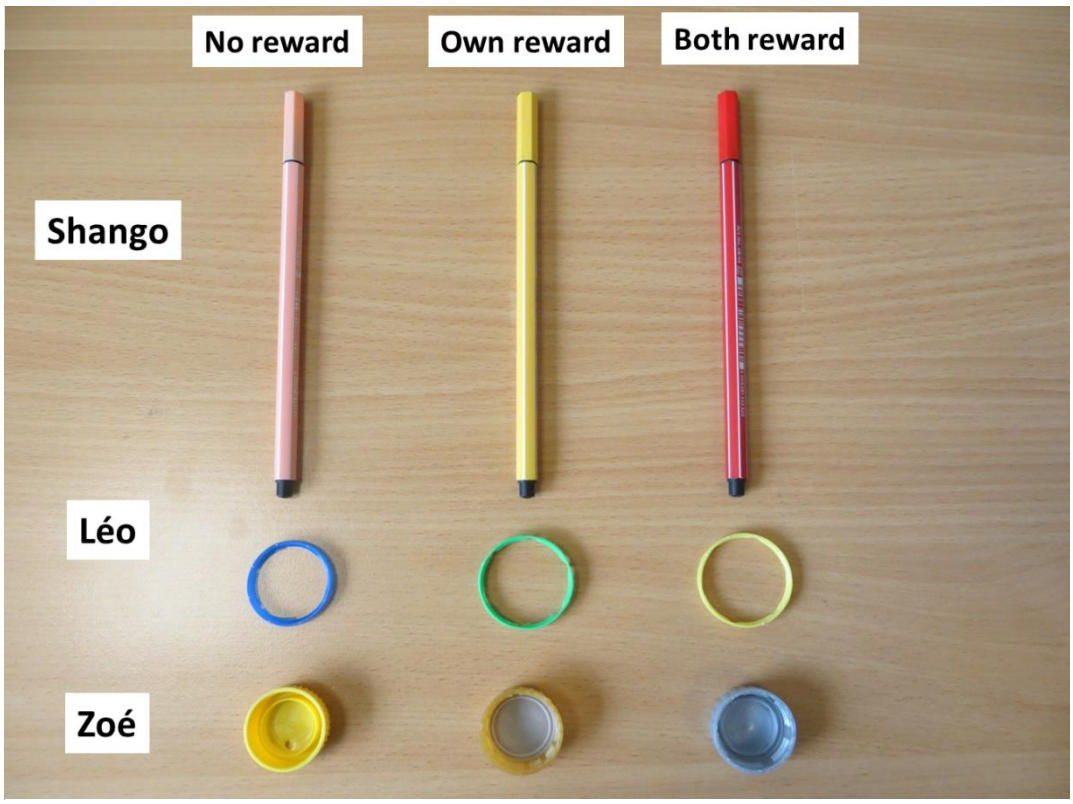

Figure 15. Experiment 1_set 3 (African grey parrots)

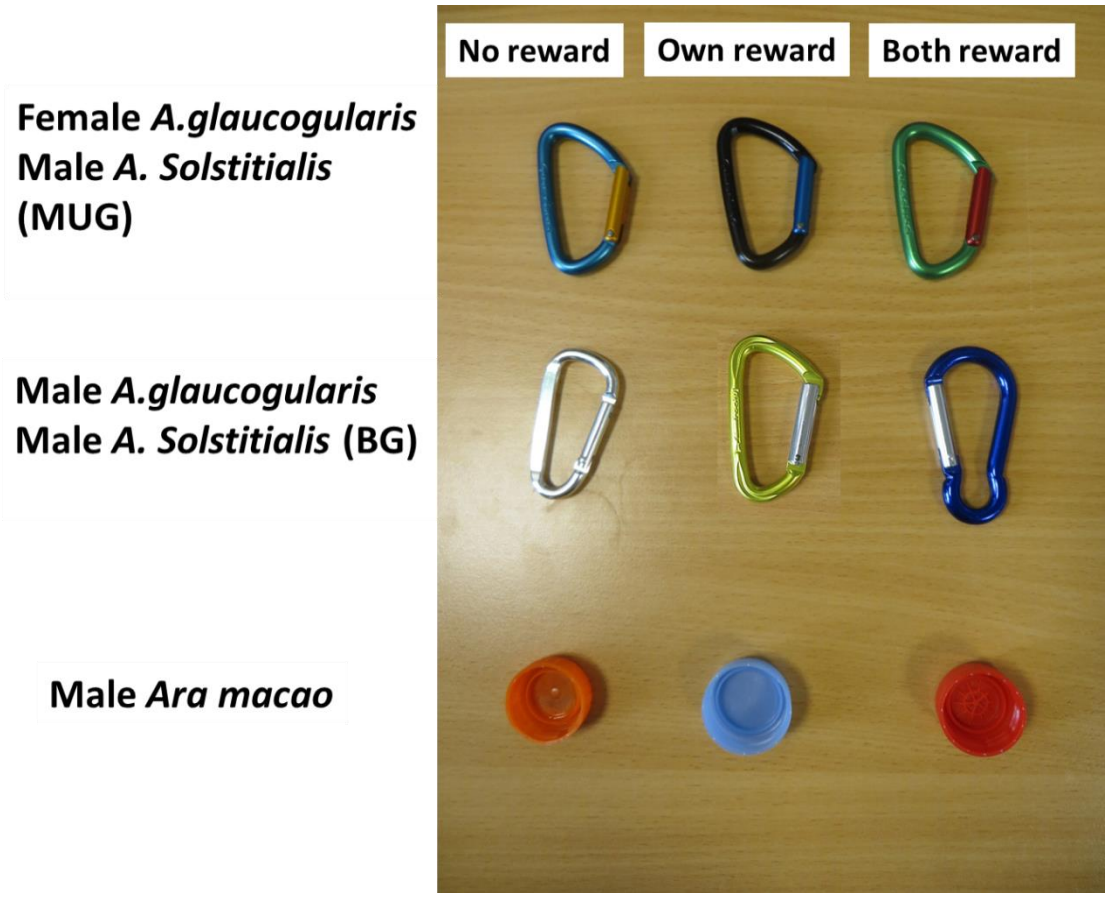

Figure 16. Experiment 1_set 2 (Other parrots)

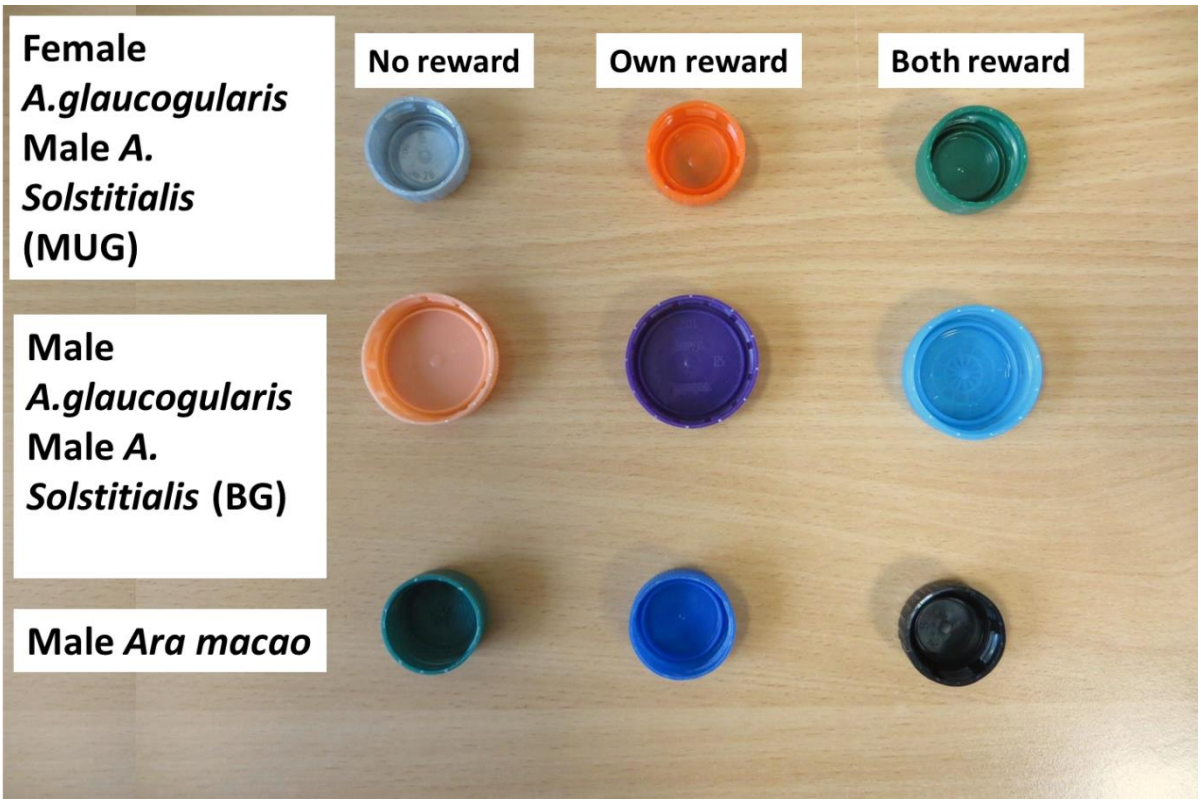

Figure 17.Experiment 1_set 2 (Other parrots)

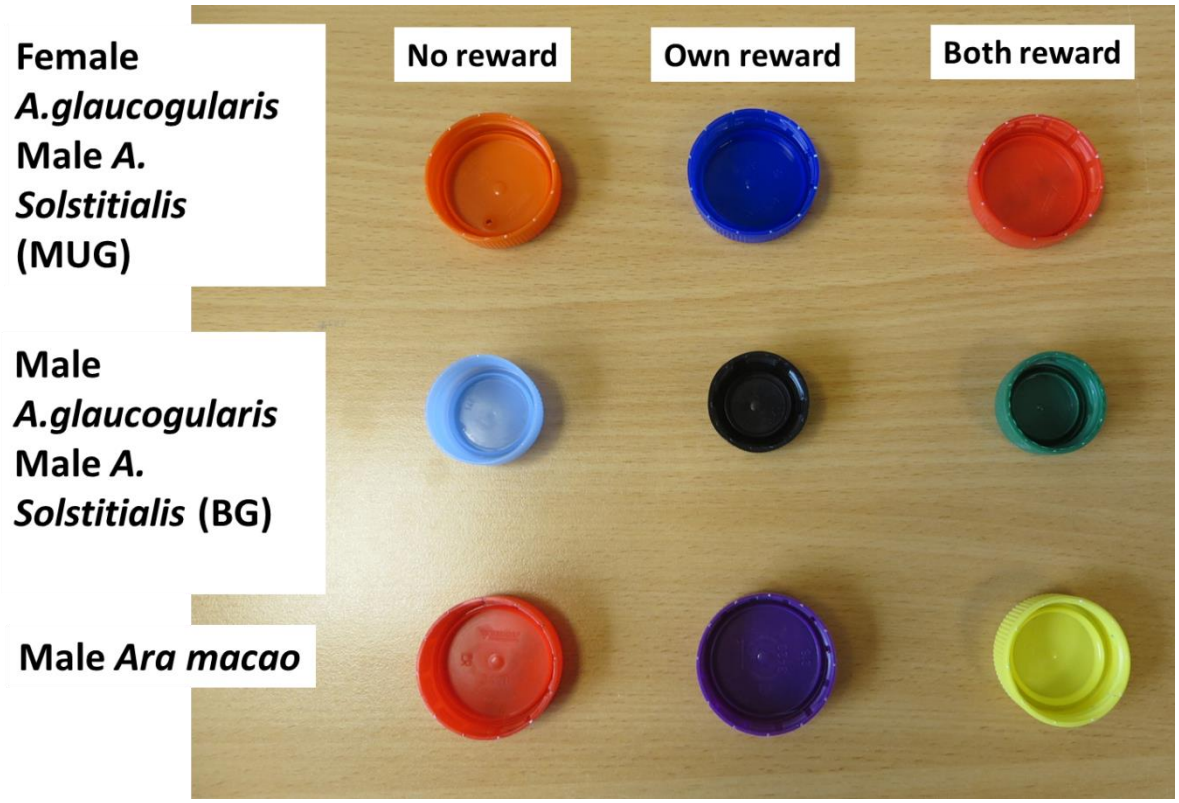

Figure 18. Experiment 1_set 3 (Other parrots)

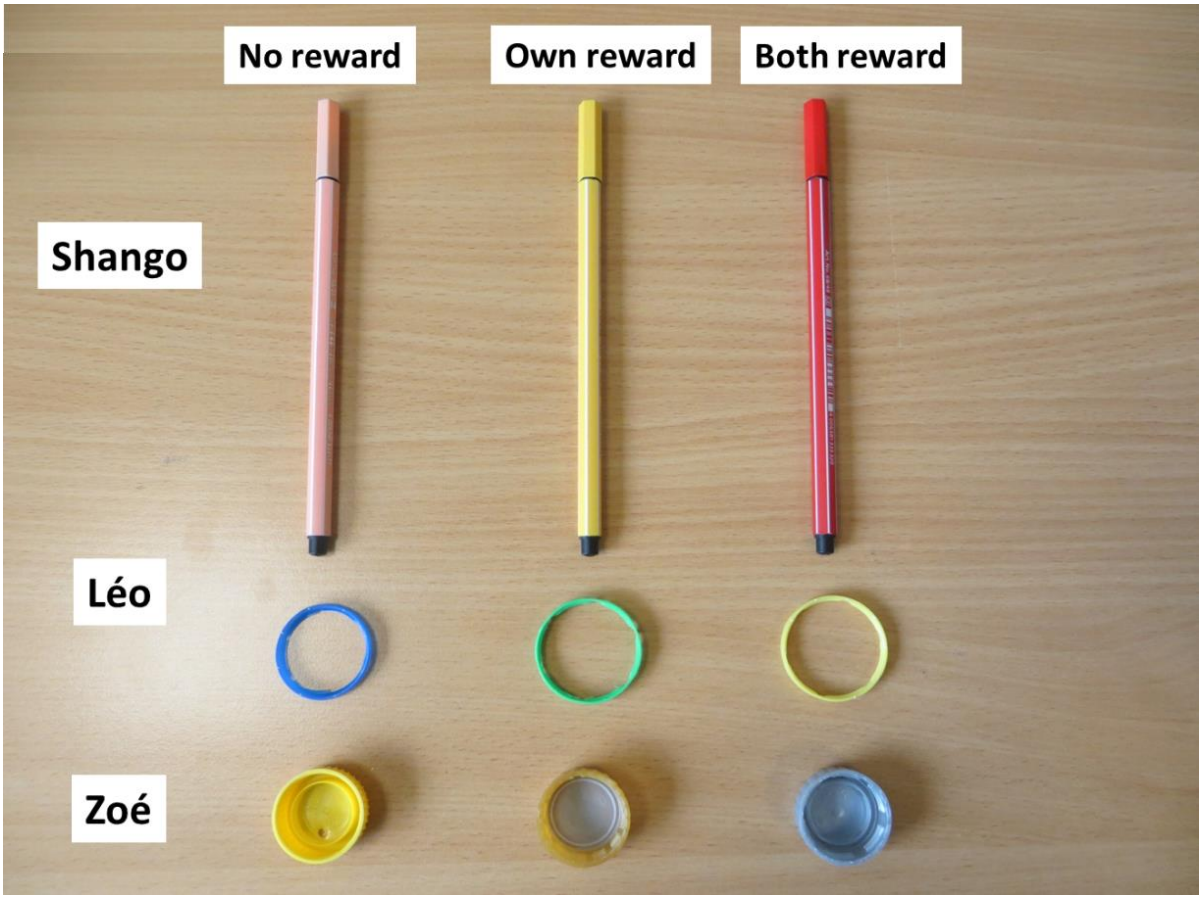

Figure19. Experiment 2 (African grey parrots)

Figure 20. Experience 3 (African grey parrots)

Study 4: Impact of social contexts on novel object exporation in jackdaws

General experimental procedure

In the present study, we investigated novel-objects exploration in neophobic jackdaws (*Coloeus monedula*) in different social contexts. Birds were either tested alone, with their mate or with a familiar opposite-sex non-partner. Twenty captive jackdaws (see Table 6) were exposed to six different conditions: a control, in which preferred food was presented in a bowl and random exposure to novel objects of 5 different categories which were presented next to the food and which differed in size and intimidation factor. Two conditions were classified as "non-intimidating" situations (control and the smallest object category) whereas the other 4 object categories were considered to represent intimidating situations.

Group	Subject	Sex	Partner (sex)	Partner index of association	Non-partner (sex)
1	Tschok	M	Jackomo (F)	0.090	Choctaw (F)
1	Jackomo	F	Tschock (M)	0.090	Chapa (M)
1	Mohawk	M	Cherokee (F)	0.035	Pronto(F)
1	Cherokee	F	Mohawk (M)	0.035	Bunny (M)
1	Blackfoot	M	Choctaw (F)	0.313	Gru (F)
1	Chocktaw	F	Blackfoot (M)	0.313	Tschock (M)
1	Chapa	M	Gru (F)	0.206	Jackomo (F)
1	Gru	F	Chapa (M)	0.206	Blackfoot (M)
1	Bunny	M	Pronto (F)	0.235	Cherokee (F)
1	Pronto	F	Bunny (M)	0.235	Mohawk (M)
2	Mokka	M	Mono (F)	0.078	Cyclop (F)
2	Mono	F	Mokka (M)	0.078	Pirate (M)
2	Tassilo	M	Hedwig (F)	0.555	Udo (F)
2	Hedwig	F	Tassilo (M)	0.555	Chimney (M)
2	Pirate	M	Dohli (F)	0.125	Mono (F)
2	Dohli	F	Pirate (M)	0.125	Moony (M)
2	Chimney	M	Udo (F)	0.070	Hedwig (F)
2	Udo	F	Chimney (M)	0.070	Tassilo (M)
2	Moony	M	Cyclop (F)	/	Dohli (F)
2	Cyclop	F	Moony (M)	/	Mokka (M)

Table 6. **Details about the subjects, partners and non partners**: sex (F: Female; M: Male), index of affiliation shared with the partner and number of different objects seen per bird. † Cross indicates bird that died during the

Degree of affiliation

The jackdaws in the groups were all clearly pair-bonded, with most pair bonds existing over a long period (>5years). Although these pair bonds and affiliative relationships were easily recognizable and well established in the two groups, 34 ad-libitum sessions of observation were carried out, 17 sessions for each aviary (Altmann, 1974) for additional confirmation. Each session lasted for 20 minutes and the number of allopreening, allofeeding, agonistic behaviors (pecking) and proximity events were recorded. A proximity event was when two birds were close enough to touch each other. The event ended when one of the two birds moved away from the other. An allopreening event was counted when a donor preened the receiver's head or back. It stopped with the donor lifting its head. An allofeeding event occurred when one individual, usually the male, actively placed food into the open beak of his partner. The allofeeding events ended when the donor removed his head from the recipient's beak.

For each dyad, we constructed an index of affiliation following Silk et al (2006) and adapted to birds by Boucherie et al (2016) (See Table 6). Recorded behaviours were: the occurrences of spatial proximity (PROX, i.e. the distance between two birds was so small that they could touch each other), and the number of affiliative behaviours, which included the number of allofeeding (FEED) and the number of allopreening (PREEN). We created the index as follow:

$$S_{ab}: \frac{((PROX_{ab}/PROX)+ (PREEN_{ab}/PREEN) + (FEED_{ab}/FEED)) \times 100}{3}$$

With S_{ab}, the index of affiliation of the ab dyad (with "a" the subject and "b", its partner); $PROX_{ab}$ the dyadic frequency of spatial proximity for the ab dyad, divided by PROX which equals to the overall mean frequency for all possible dyads (and similarly for the other

variables: FEED and PREEN). The denominator was fixed and refers to the number of variables. The value of the index of affiliation increased with the strength of a relationship.

The indexes only took into account birds from the same aviary, consequently partners and non-partners were all familiar birds from the same aviary.

Consequently, we considered those birds as mated-pairs , which exhibited the highest index of association, with the exception of Moony and Cyclop, from the second aviary. These two birds formed a mated pair, but Cyclop was very shy and therefore did not behave naturally in the presence of the human observer. Cyclop hid from the observer most of the time and consequently she and her partner were never observed to allofeed or allopreen each other during the observation sessions.

To create non-partners dyads, we paired together males and females from the same aviary that were not mates, avoiding dyads that displayed aggressive interactions. We attempted to choose birds that showed similar patterns of boldness towards humans and novelty in.

Material

The apparatus consisted of a bowl filled with preferred food (i.e. food not available *at libitum*, see below) and a novel object to jackdaws when they were tested either with their mate, with a non-partner of the opposite sex or alone.

A ceramic bowl (diameter: 14 cm) was filled with preferred food that birds could only obtain during the test: 10 pieces of crunchy muesli (Knusper müsli Crownfield ®) and 10 halves zoophoba larvae (*Zophobas morio*). The bowl was placed on the floor of the testing compartment (aviary 1: ca. 2m x 2m x 3m; aviary 2: ca. 1.50 m x 3 m x 3 m) in the center of a large circle (60 cm in diameter) split into 2 zones of approach drawn on the floor with a piece of white chalk (Figures 21a & b). A perch (approximatively 120 cm long, 5 cm of diameter) was attached to one wall of the test compartment at ca. 1.20 cm height and touched the floor

on the other side within the central zone of the circle to facilitate the birds' approach to the food bowl (see Figures 21a & b).

Figure 21. Experimental set-up in (a) aviary 1 and in (b) aviary 2. A perch was hung on the wall to the floor to help birds to go to the bowl in each aviary. The large circle was 60 cm diameter. Food bowl was always filled with the same amount of food and the novel object was put inside the bowl.

The jackdaws were tested with five categories of novel objects (Figure 22) chosen according to a hypothesized increasing "intimidating effect". Starting from (1) non-intimidating tiny plastic figurines of ca. 3,5cm (1 = "foot toys"; Stikeez Football euro 2016 ® 3.5 x 1.2 cm), to gradually increasing in size and liveliness to (2) bigger plastic toys (2 = bath toys; approximately 5 x 5 cm) and (3) even bigger soft plush toys (approximately 8 x 10 cm), followed by (4) moving objects, potentially perceived as animated ("hexbugs" moving toys mimicking insects' movements; Hexbug Nano ®; size: 4.5 x 1.5x 1.5 cm) and culminating in (5) schematic pictures of eyes printed in black and white on a piece of cardboard (approximatively 16 x 10.7 x 0.3 cm).

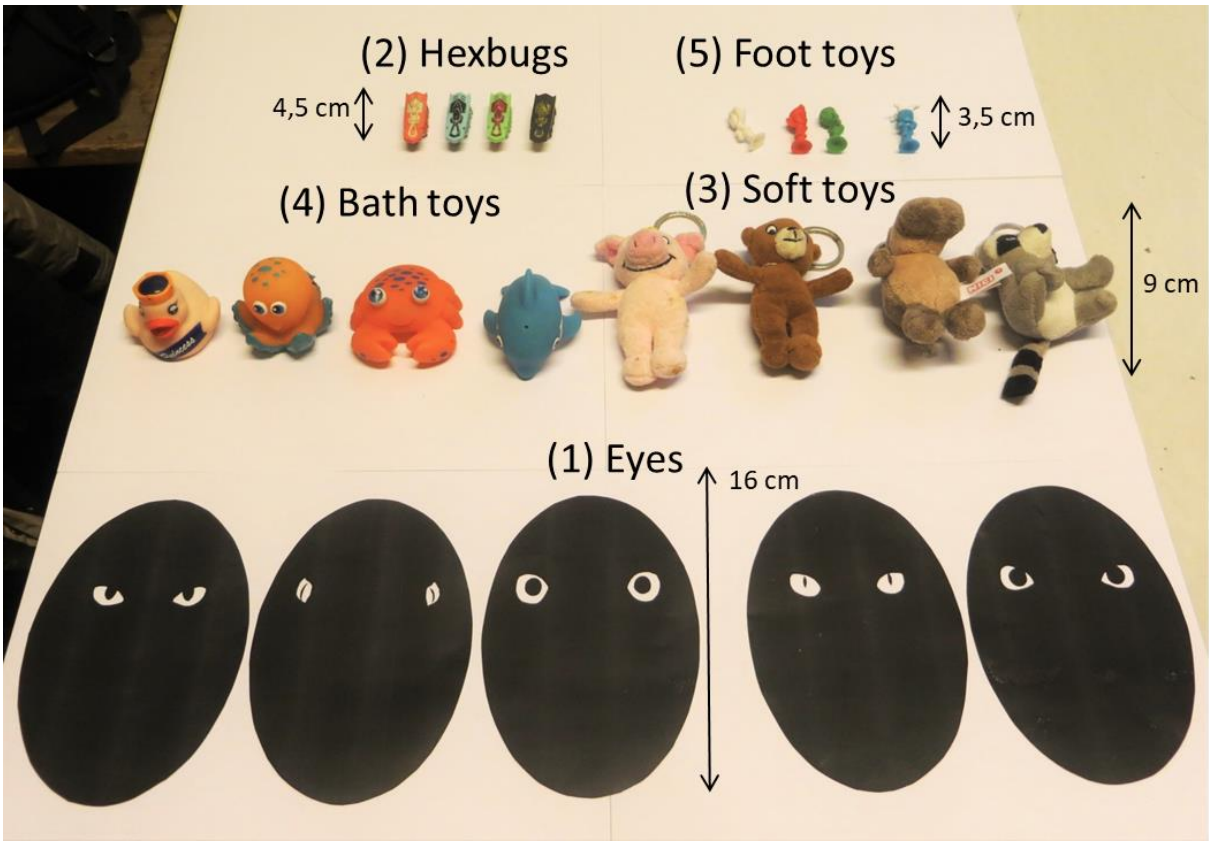

Figure 22. The five categories of novel objects presented during the test sessions, numbered in an order starting from the potentially most intimidating stimuli to the least or non intimidating ones: (1) schematic eyes, (2) moving hexbugs, (3) soft toys, (4) bath toys and (5) foot toys. Each bird saw a different object of each category in each condition (alone, partner, non-partner) in order to prevent habituation.

In the test conditions, the experimenter put each object in the bowl together with the food except for the eyes, which were attached vertically to the bowl with some tape. While the bowl with the eyes was introduced in the aviary for the test, the eyes were covered by a black plastic bag. It was removed just after that the bowl was put on the testing compartment. In the control condition, the bowl was only presented with food.

Procedure

All individuals/dyads were tested in testing chambers, to which they were well habituated, in visual isolation from their main aviary. Three of such testing compartments were linked to the main aviary: the waiting compartment, an intermediate compartment and the testing compartment, all of which were interconnected through doors but were all visually blocked from one another and from the main aviary by opaque walls/doors. At the beginning of the testing phase, the entire group moved into the waiting compartment. This was a previously trained, well-established routine; the experimenter entered the aviary giving some specific vocal commands encouraging the birds to fly into the waiting compartment. Next, the experimenter entered from the testing compartment's side, and made the chosen pair enter in the testing compartment. Consequently, even if the birds waiting to be tested were close to the testing compartment, they were not visible by the tested subjects and could not interact with them during the experiment. Each compartment was covered by black tissue in order to avoid any disturbance from the non-tested birds present in the aviaries, and to prevent the subjects to interact with other animals than the conspecifics paired with them.

Each pair was introduced in the testing compartment. The experimenter started the video recording, allowed the chosen subjects to enter the testing compartment and then left the compartment through the main door. Then, the experimenter introduced a ceramic food bowl covered by a small plate through a small opening in the door by reaching in with her arm.

When the bowl was stood at right place (indicated by a chalk mark drawn on the floor), the experimenter removed the cover from the bowl, and retracted her arm from the compartment. The test started at the precise moment when the experimenter removed the plate from the food bowl, allowing the birds' access to it (Figures 21 a & b). Each test was 20 minutes long and was recorded with a camera (SONY HDR-CX220E) screwed onto the testing compartment's wall via a metallic trail camera wall mount (FRIBEND® a 36).

The order of testing of each pair was randomized to reduce the bias due to the time spent waiting before being tested and the food motivation, since birds did not have access to food in the waiting compartment (maximum time without *ad libitum food*: 80 minutes). Likewise, the testing period (morning or afternoon) was also randomized so as to avoid any effect on the bird's behavior potentially caused by the time of the day. The order in which the objects were presented was pseudo-randomized and counterbalanced in each session too. During the first part of the experiment (12^{th} of July-27^{th} of July 2016) all birds were tested with 3 of the objects (soft toys, bath toys and hexbugs) and in the control condition (no object). In the second part of the experiment (19^{th} -27^{th} of August 2016), they were tested with the two remaining objects (foot toys and eyes). The birds were tested once a day (either in the morning or in the afternoon) during the first part and twice a day in the second part of the experiment.

Since each bird was tested in the three conditions (i.e. with their mate, with an opposite-sex non-partner bird and alone) in each category, each individual was exposed to three different objects per category to avoid habituation. Objects of the same categories were comparable in size and overall appearance (Figure 22) and each bird saw each object only once. Overall, each bird received 18 tests (5 objects and a control in each of the three conditions: with a partner, with a non-partner and alone). Two birds (Choctaw and Gru) died through an accident before the beginning of the second session and were only tested with 3 objects (soft

toy, bath toy and hexbug) and in the control condition. As a consequence, Chapa (Gru's partner) was tested with all objects but could not be tested in the "partner condition" thus participating in 16 instead of 18 tests. In the case of Blackfoot (Choctaw's partner) only 14 tests could be conducted because, he lost both his partner and non-partner. Also, an error in randomization sheet occurred so that Pronto was not tested alone in the bath toy category.

Recorded behaviors

The videos were analyzed using the software VLC media player, version 1.5, to assess the exploratory behavior of each subject during the tests. It was recorded whether the birds entered the large circle, whether they ate, whether they touched the object (except in the control condition) and whether they removed the object (except in the control condition). Latencies (in seconds) to enter in the large circle, to eat, to touch the object and to remove the object were also recorded. Finally, the number of times birds touched the object was recorded. To verify whether subjects were more often near their mate than near the non-partner during the tests, we also recorded the number of proximity events, e.g. how many times the two birds were close enough to touch each other. Finally, we recorded the number of aggressive behaviors (pecking and threatening displays) expressed by the subject toward the bird it was tested with (their mate or a non-partner).

Statistical analysis

Firstly, we checked whether subjects were seen more frequently near their mate and were less aggressive to them than to their non-partner during the tests. In order to investigate this question, we ran generalized linear mixed models (GLMMs) using a Poisson distribution with a maximum likelihood estimator to investigate what impact the condition (partner or non-partner), the object category (intimidating or not) and their interaction had on the number of

proximity events within dyads and the number of aggressive behaviors displayed by each bird toward the other bird with whom it was tested. The effect of sex and the effect the interaction between sex and condition on the number of aggressive behaviors were also tested. The level of intimidation of the object categories was classified into two levels (intimidating or not) instead of six levels (control, foot toy, bath toy, soft toy, hexbug and eyes) to allow us to test for interaction with other terms of the models without model convergence failure. The classification was based on mean probabilities and mean latencies to reach the large circle and to eat for each object and in the control situation. Because there was no object in the control situations, we did not use the probabilities and latencies to touch and to remove the object to do the classification. Overall, mean probabilities were higher and mean latencies were shorter in the control and the foot toy situations than in the other situations. Consequently, we refer to these two classifications of object categories as "situation"; the control and the foot toy categories were considered as the non-intimidating situation while the other categories were classified as intimidating situations. Models also included the group of birds (aviary 1 or 2), the day of testing, the order of tests (from 1 to 18) as random effects. The dyad nested within the aviary was also added as a random effect to avoid pseudoreplication because we have repeated measures for each dyad. The complete model (i.e. including an interaction between condition and situation) was first fitted and then the interaction was removed if it was not significant. The significance of a term in the model was assessed using the change in deviance after removal of that term (Likelihood-Ratio Test, LRT) with a chi-square test with the appropriate degrees of freedom because deviance differences are chi-square distributed. Normality of random effects and homoscedasticity and normality of residuals were checked.

Secondly, before building models to investigate condition, situation and sex effects on exploratory behavior, we used a principal component analysis (PCA) to rank the jackdaws

according to their tendency to explore because we wanted to test for the effects of the interactions between the birds' general tendency to explore and other terms of the models on exploratory behavior. This step also allowed us to verify whether the partner and the non-partner of each subject had a similar tendency to explore. We only used data recorded in the "alone" condition to avoid the effects of another bird's presence on the subjects' behavior. Four variables were used in the PCA: the latencies to reach the large circle, to eat and to touch the object and the number of times the subject touched the object. Consequently, tests in the control situation were excluded (no object to touch). The latency to remove the object was not used in the PCA because this behavior was too rare. The first principal component (PC1) axis accounted for 70.5% of the variation and scores decreased with the latencies and increased with the frequency to touch the object (see Results and Table 9). It means that a high PC1 score represents a bird that explore quickly the object and that touch frequently the object. Mean PC1 scores of each bird were thus used to rank the 20 jackdaws (from 1 to 20) according to their tendency to explore, allowing us to use these explorative ranks in subsequent analyses. Other PCA axes (PC2-PC4) were not used for subsequent analyses.

Finally, we tested whether jackdaws were more exploratory when with another bird than when alone and especially when with their mate. We then ran GLMMs using a binomial distribution with a maximum likelihood estimator to investigate how the condition (alone, with a partner or with a non-partner), the situation (intimidating or not), the sex, the explorative rank and the interactions between the condition and other terms impacts the probability of reaching the large circle, the probability of eating, the probability of touching the object and the probability of removing the object. We also ran linear mixed models (LMM) with a maximum likelihood estimator to investigate how the fixed effects described above impacted on the latencies to reach the large circle, to eat and to touch the object.

We excluded all tests in which a subject did not show the relevant behavior (latency to reach the circle: 105 tests excluded over 339; latency to eat: 128/339; and latency to touch the object: 200/339). Latencies were log transformed to read normality of residuals. Because birds rarely removed the object (27/279), we were not able to use the latency to remove the object as a response variable in our models. Lastly, we ran a GLMM with a Poisson distribution and a maximum likelihood estimator to investigate how the fixed effects described above impact the number of times a bird touched the object. All models also included the group, the day of testing, the order of tests and the individual identity nested in the aviary as random effects. The complete models were first fitted and we then removed the interactions if they were not significant. The significance of a term in the model was assessed using LRTs with a chi-square test with the appropriate degrees of freedom. Normality of random effects and homoscedasticity and normality of residuals were checked. Results are shown ±SE i.e. SE is for "standard error".

All statistical analyses were performed with R (R Development Core Team 2008) using the LME4 R package of Bates et al. (2014) to run all models.

Results

Results

Study 1: Food sharing in cockatiels

Food transfers

The cockatiels received 5180 food pieces in total. They consumed 3081 food items (59 %), dropped 1432 (28 %) and transferred 667 food pieces (13 %) from one bird to another: 90 (2%) by stealing and 577 (11%) by cofeeding.

Effect of food-type

Cockatiels shared fennel, the preferred food, significantly more via cofeeding than carrot (estimate = 0.45 ± 0.09, $p < 0.001$, dispersion parameter φ =1.5). They also dropped the less preferred food, carrot, more often than fennel (estimate = -5.89 ± 1.44, $p < 0.001$). No significant effect of food type was found for consuming (estimate = 2.30 ± 2.17, $p = 0.294$) and stealing (estimate = 0.04 ± 0.21, $p = 0.831$, dispersion parameter $\varphi = 0.79$).

Developmental pattern

The mean number of food pieces consumed or dropped by the young cockatiels, did not evolve much over time (Figure 23).

The mean number of food pieces consumed by the birds did not vary considerably across the testing periods. More food pieces were consumed in period 2 than in period 1 (estimate = 7.90 ± 2.95, $p = 0.037$) but no significant difference was found between period 1 and 3 (estimate = 6.45 ± 3.17, $p = 0.175$), period 1 and 4 (estimate = 6.03 ± 3.05, $p = 0.197$), period 2 and 3 (estimate = -1.45 ± 3.17, $p = 0.968$), period 2 and 4 (estimate = -1.87± 3.05, $p = 0.928$) and period 3 and 4 (estimate = -0.42 ± 3.22, $p = 0.999$).

Regarding the mean number of food pieces dropped over the study periods, we observed a slight increase over time. There was a tendency for the birds to drop more food items in

period 3 than in period 1 (estimate = 5.16 ± 2.11, p = 0.070). Moreover, birds dropped significantly more food pieces during period 4 than during period 1 (estimate = 8.59 ± 2.03, p < 0.001) and during period 3 than during period 2 (estimate = 6.01 ± 2.11, p = 0.023).

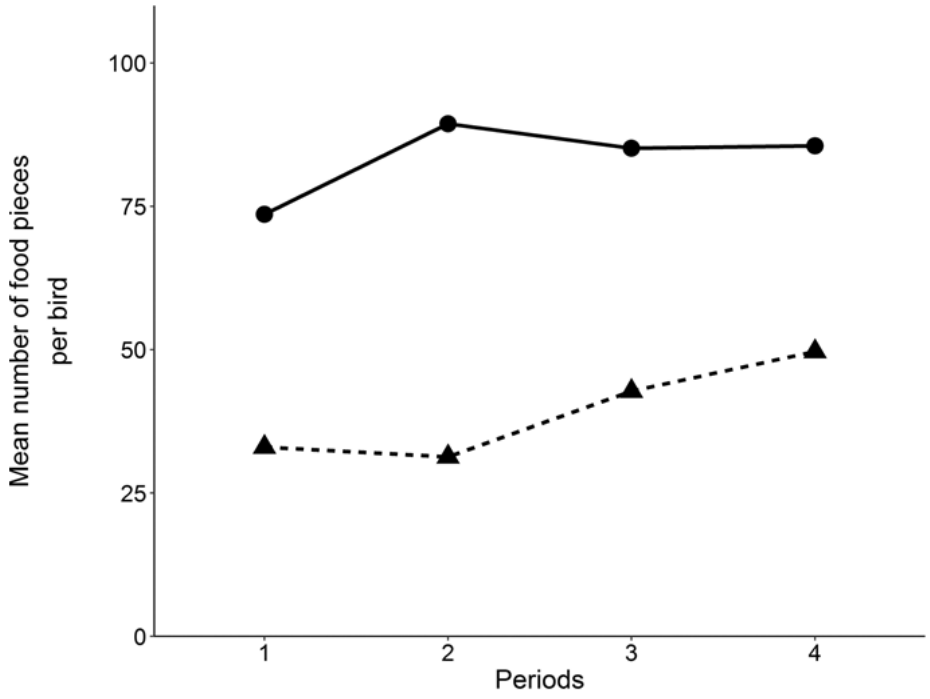

Figure 23. Mean number of food pieces consumed (●) and dropped (▲) per bird over the 4 periods of test.

The mean number of food pieces transferred between young cockatiels, both through food-sharing i.e. cofeeding and stealing events, strongly decreased over time (Figure 24).

Stealing events were generally scarce but still decreased over time. There was a significant decrease between period 1 and period 3 (estimate = -1.28 ± 0.37, p < 0.001), between period 1 and period 4 (estimate = -2.37 ± 0.60, p < 0.001) but also between period 2 and 3 (estimate = -1.17 ± 0.38, p = 0.009) and between period 2 and 4 (estimate = -2.27 ± 0.60, p < 0.001). No significant difference was found between period 1 and 2 (estimate = -0.10 ± 0.23, p = 0.965) and between period 3 and 4 (estimate = -1.09 ± 0.67, p = 0.329).

Cofeeding decreased significantly over time. We observed significant differences between all testing periods: period 1 vs 2 (estimate = -0.63 ± 0.11, $p < 0.001$), period 1 vs 3 (estimate = -1.13 ± 0.14, $p < 0.001$), period 1 vs 4 (estimate = -1.95 ± 0.19, $p < 0.001$), period 2 vs 3 (estimate = -0.49 ± 0.13, $p = 0.001$), period 2 vs 4 (estimate = -1.32 ± 0.18, $p < 0.001$) and period 3 vs 4 (estimate = -0.83 ± 0.19, $p < 0.001$).

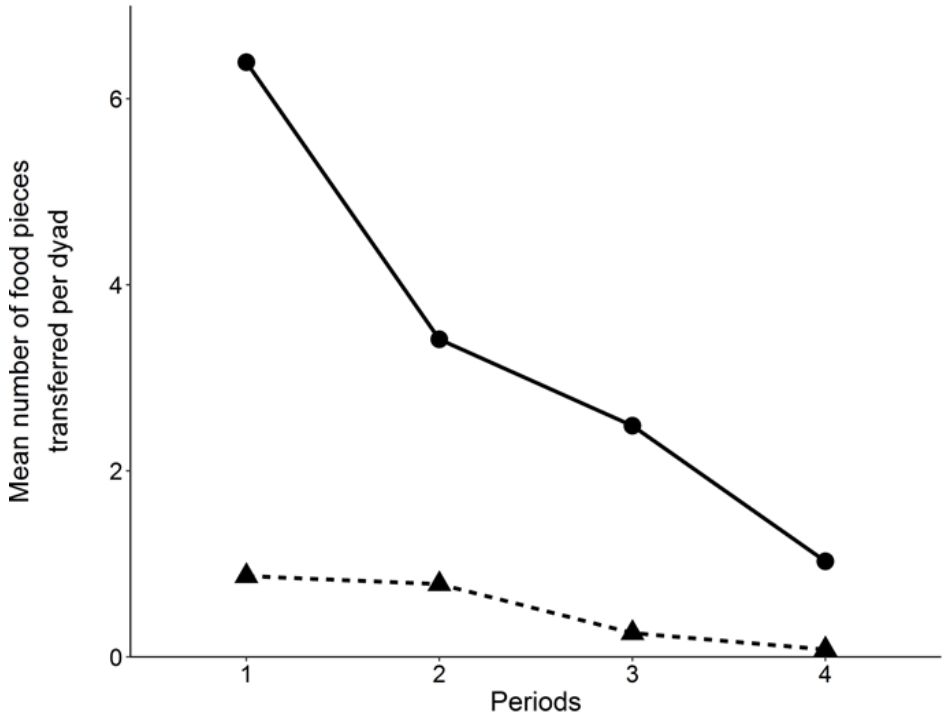

Figure 24. Mean number of food pieces transferred per dyad via cofeeding (●) and stealing (▲) over the 4 periods of test.

Number of sharing partners over time

The mean number of cofeeding sharing partners per bird also decreased over time (Figure 25): it significantly diminished between period 1 and period 4 (mean number of partners in period 1= 3.87± 0.58 vs 2 ± 0.49 in period 4; estimate = -0.68 ± 0.32, $p = 0.033$, $\varphi = 0.73$) but not between other periods. The same pattern was found with stealing events (mean number of partners in period 1 = 1.9 ± 0.35vs 0.33± 0.16 in period 4; period 1 vs 4: estimate = -1.73 ± 0.62, $p = 0.005$, $\varphi = 0.82$).

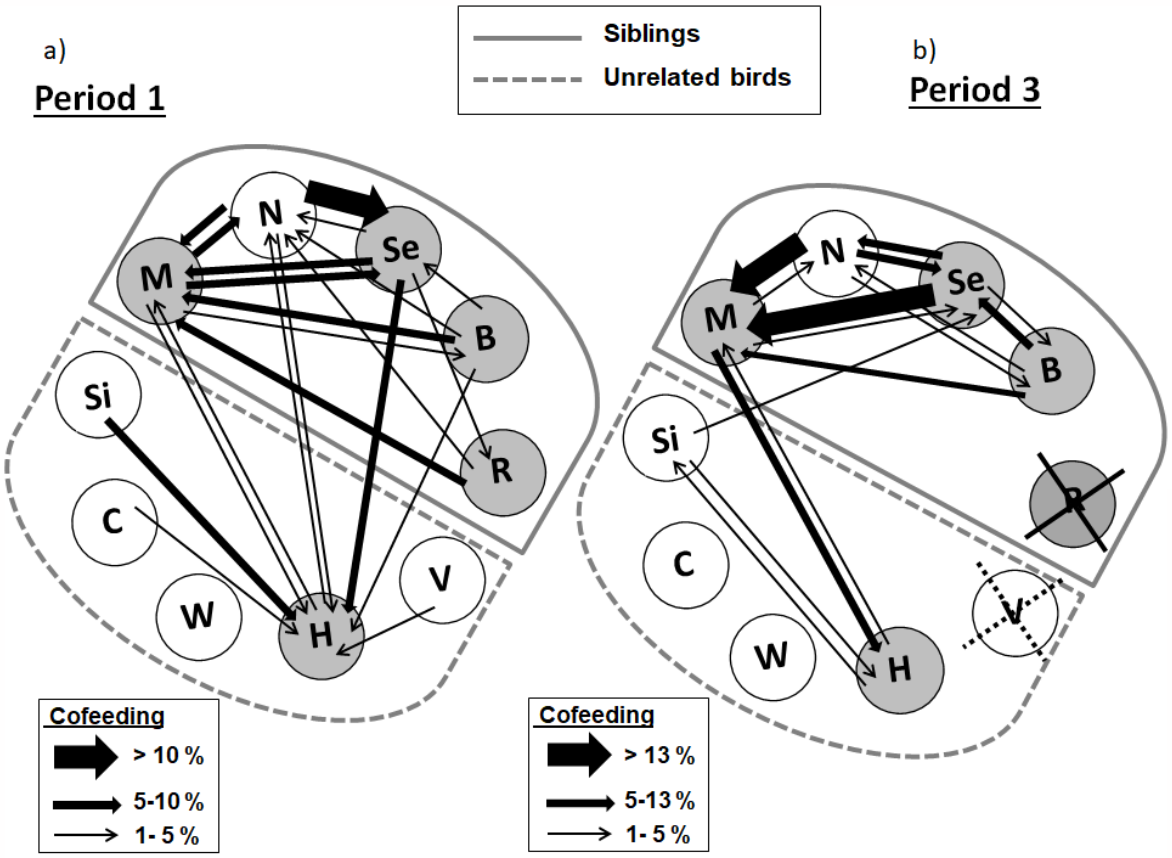

Figure 25. Sociogramm depicting the direction and frequency of cofeeding throughout (a) Period 1 and (b) Period 3. Each circle represents an individual cockatiel and every letter identifies each individual as a short version of its name. The color of the circle indicates the sex (grey: male, white: female). The filled cross on an individual circle indicates bird who died during the experiment. The broken cross indicates bird who did not participate as a donor. The weighting of the arrows indicates frequency of interactions as a percentage of the total occurrence of cofeeding within the group.

Kinship and sex effects on cofeeding and stealing

Birds shared more food with siblings than with unrelated birds (estimate = 1.43 ± 0.49, p = 0.004) while no effect of kinship was found regarding the stealing strategy (estimate = 0.55 ± 0.36, p = 0.133)(Figure 26).

The receiver's sex had no influence on cofeeding frequency (estimate = 0.43 ± 0.57, p = 0.661) but males stole more food from each other (estimate = 0.88 ± 0.37, p = 0.016) than in heterosexual pairs, yet considering that no stealing events occurred between females.

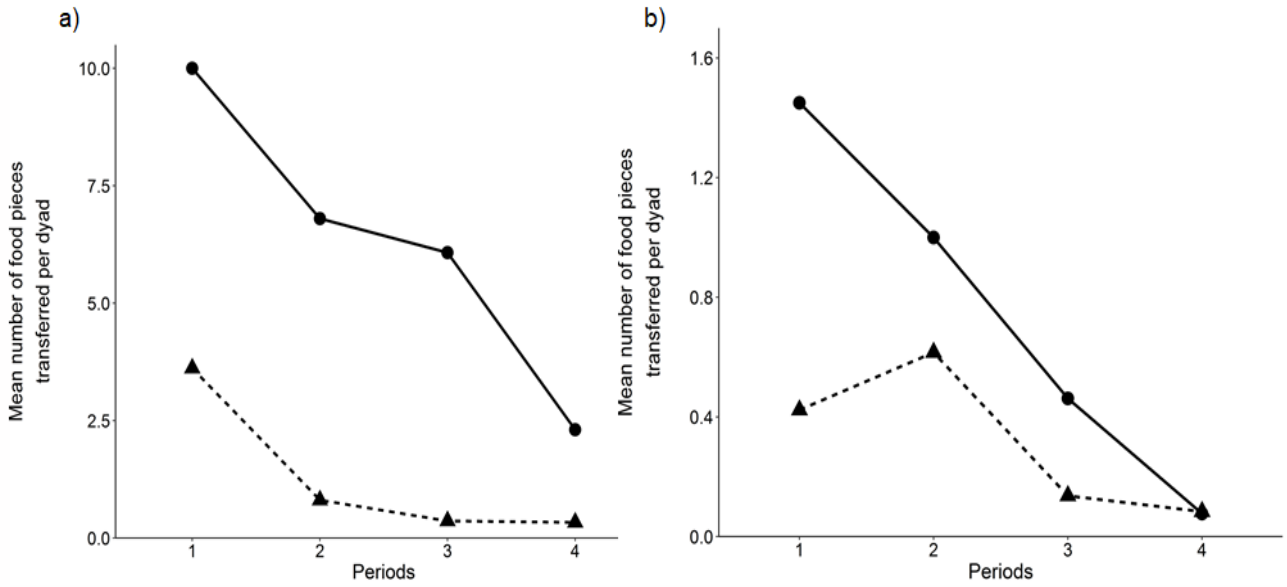

Figure 26.(a) Mean number of food pieces shared via cofeeding per dyad between siblings(●) and non-siblings (▲) over the 4 periods of test. (b) . Mean number of food pieces stolen per dyad between siblings(●) and non-siblings (▲) over the 4 periods of test

Reciprocity and interchange

The matrix analysis of cofeeding showed that cockatiels reciprocated food-transfers,(TauKr = 0.644, N = 9, $p < 0.001$). No reciprocity was observed regarding stealing events (TauKr = 0.084, N = 10, p = 0.301). We also observed an increase in the percentage of allopreening between two brothers, Seth and Merlin with their sister Nephtys over time (Figure 27).

Finally, we investigated if the cofeeding and stealing matrices were correlated with the matrices of allopreening. We observed a positive correlation between the cofeeding and allopreening matrices, meaning that donors shared food with individuals from whom they received allopreening (TauKr = 0.342, N = 10, $p < 0.001$). There was also a positive correlation between the stealing and allopreening matrices (TauKr = 0.235, N = 10, p = 0.013).

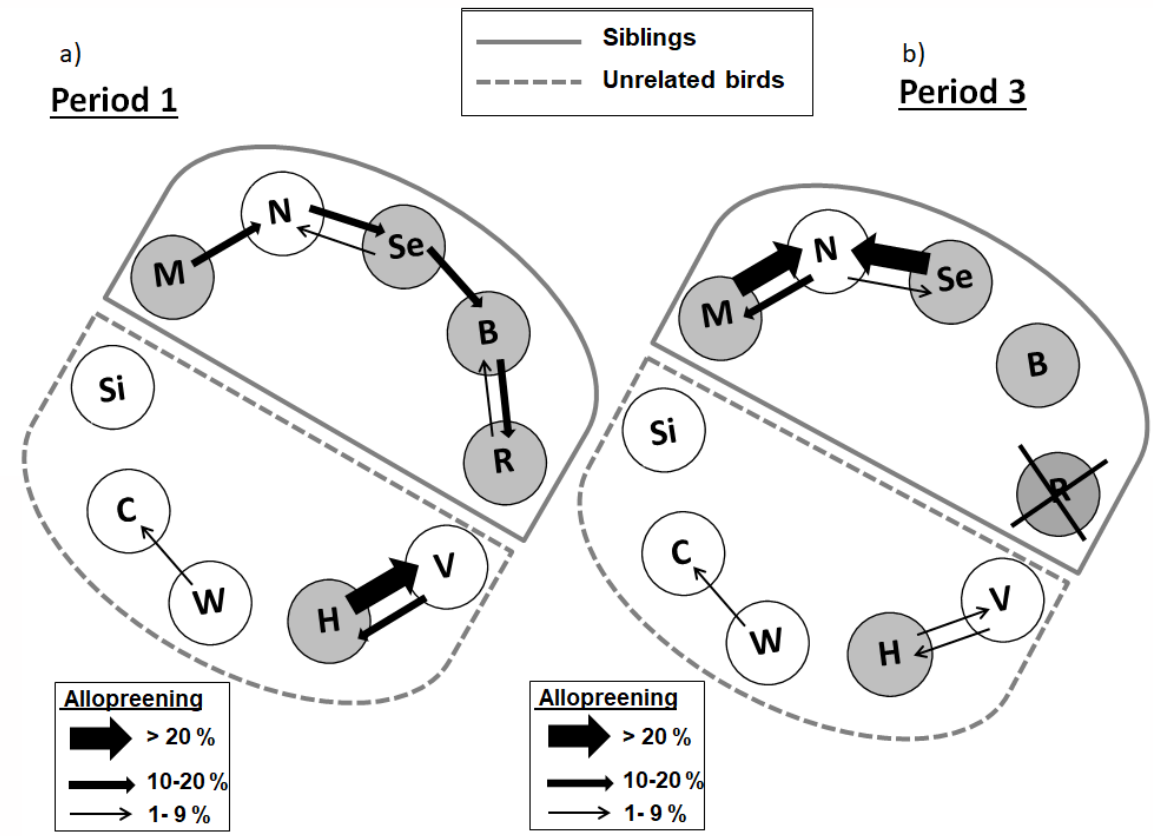

Figure 27. Sociogramm depicting the direction and frequency of allopreenings recorded during affiliative sessions corresponding at (a) Period 1 and (b) Period 3 of the food-sharing experiment. Each circle represents an individual cockatiel and every letter identifies each individual as a short version of its name. The color of the circle indicates the sex (grey: male, white: female). The filled cross on an individual circle indicates bird who died during the experiment. The weighting of the arrows indicates frequency of interactions as a percentage of the total occurrence of cofeeding within the group.

Study 2: Emotional response to conspecific distress calls in cockatiels

1. *Impact of the phase ("before", "during" and "after" the playback stimulus) on the birds' behaviour*

First, regarding the birds' activity (number of zone changes), the cockatiels were more active during the playback stimuli than before (estimate = -3.73 ± 0.60, z = -6.16, $p < 0.0001$) and after (estimate = -1.36 ± 0.10, z = -14.05, $p < 0.0001$) stimulation (dispersion parameter φ = 2.52). Post hoc analysis revealed that the birds were also more active after the playback stimuli than before stimulation (Tukey test, $p < 0.0001$; see Figure 28A).

Second, the phase of the experiment had a significant effect on the number of calls the subjects produced. Indeed, no calls were emitted before the playback stimuli and there were more calls emitted during the playback stimuli than after stimulation *(*estimate = -2.38 ± 0.35, z = -6.82, $p < 0.0001$, φ = 0.83; see Figure 28B).

Third, we observed no significant effect of the phase on the time spent in zone 1 (during - before: estimate = 0.30 ± 0.56, z = 0.54, p = 0.59, φ = 0.95; during – after: estimate = 0.23 ± 0.38, z = 0.60, p = 0.55; after – before: Tukey test, p = 0.99; see Figure 28 C).

Fourth, concerning the crest position, it appeared that the cockatiels exhibited crest position 1 (i.e. the feathers erected maximally on top of their head) more during the playback stimuli than before (estimate = -3.78 ± 1.03, z = -3.68, $p < 0.001$, φ = 0.75) and after stimulation (estimate = -1.12 ± 0.48, z = -2.36, p = 0.018). The birds also exhibited crest position 1 more after the playback stimuli than before stimulation (Tuckey test, p = 0.018; Figure 28 D).

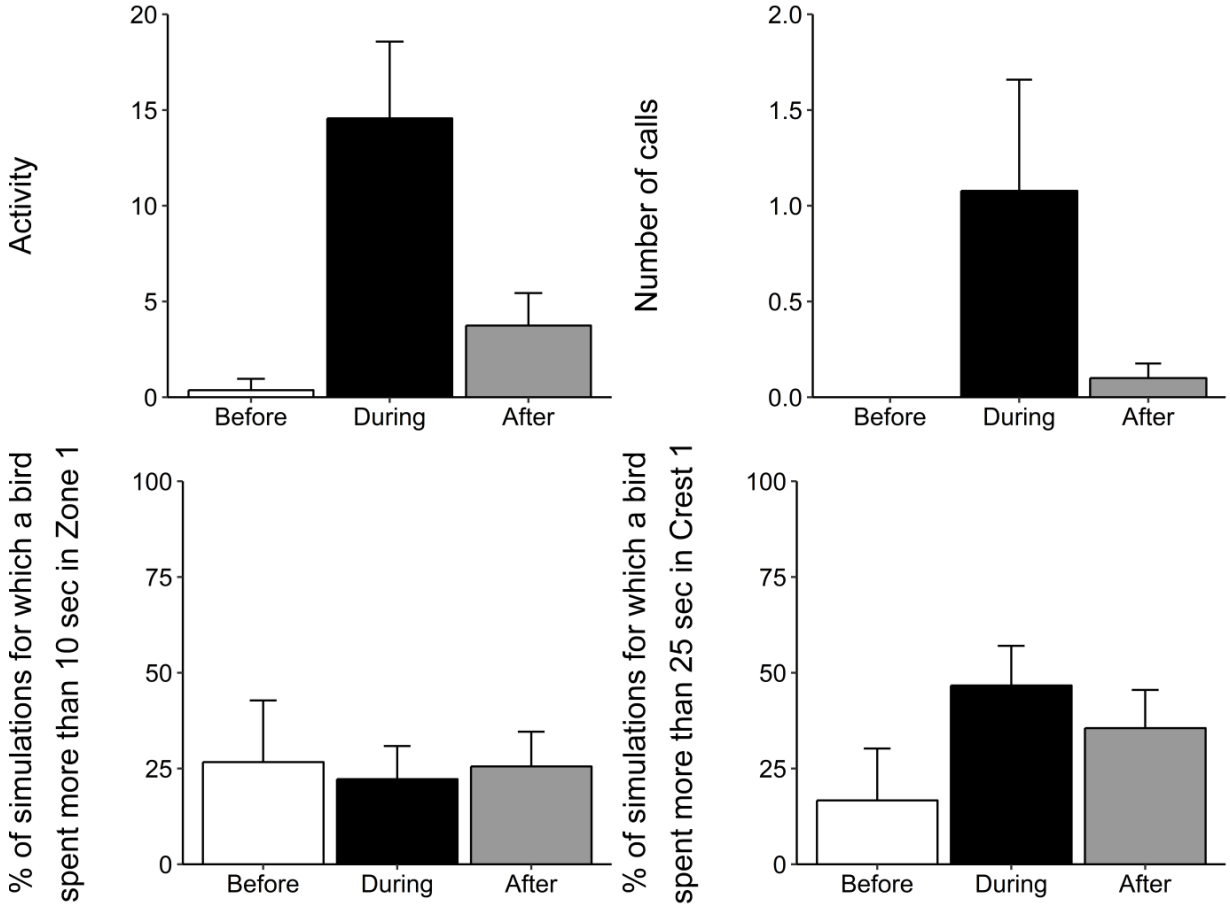

Figure 28. **Least square means ± SE. of (A) activity i.e. the number of zone changes by the subject, (B) number of calls, (C) Percentage (%) of audio stimulations for which the subject spent more than 10 seconds near the loudspeakerand (D) Percentage (%) of audio stimulations for which the subject spent more than 25 seconds in crest 1 in the phases before, during and after the playback stimuli.** Statistical differences between conditions (before, during, after) are given (*** = $p < 0.001$; **= $p < 0.01$; *= $p < 0.05$). (A) Activity: before 0.37 ± 0.31, during 14.57 ± 2.05, after 3.74 ± 0.87. (B) Calls: before 0± 0, during 1.08 ± 0.30, after 0.10 ± 0.04. (C) Zone: before 27± 8.21, during 22 ± 4.41, after 25.6 ± 4.62. (D) Crest: before 16.7 ± 6.92, during 46.7 ± 5.29, after 35.55 ± 5.07

Behavioural responses to the different playback stimuli (partner, non-partner, white noise)

1.1. During playback stimuli

When looking only at the behaviours occurring during the playback stimuli, cockatiels were more active when confronted with a partner's distress call than with a non-partner's call (estimate = -0.22 ± 0.10, z = -2.30, p = 0.022, φ = 2.22) or white noise (estimate = -0.97 ± 0.12, z = -8.05, p < 0.0001). Subjects were also more active during a non-partner distress call playback during white noise (Tukey test, p < 0.0001, Figure 29A).

Concerning the calls produced by the subjects, the birds emitted more calls during the playback of distress calls than during playback of artificial white noise (partner – white noise: estimate = -1.22 ± 0.44, z = -2.80, p = 0.005, φ = 0.82; non-partner – white noise: Tukey test, p = 0.002). However, no significant difference was found in the number of calls emitted when a partner or a non-partner distress call was played back (estimate = 0.19 ± 0.31, z = 0.63, p = 0.53, Figure 29B).

Moreover, birds spent less time near the loudspeaker during the playback of partner distress calls than during non-partner distress call playbacks (estimate = 3.76 ± 1.90, z = 1.98, p = 0.05, φ = 0.65). They also avoided this zone more during a partner distress call or a non-partner distress call playback than during artificial white noise (partner – white noise: estimate = 6.32 ± 2.17, z = 2.92, p = 0.004; non-partner – white noise: Tukey test, p = 0.04, Figure 29C).

Finally, birds displayed crest position 1 more often while listening to a partner distress call playback than to that of non-partner distress call (estimate = -1.98 ± 0.93, z = -2.13, p = 0.033, φ = 0.73) or white noise (estimate = -2.69 ± 0.98, z = -2.74, p = 0.006). However, there was no significant difference in time displaying crest position 1 between non-partner distress calls and artificial white noise playbacks (Tukey test, p = 0.644, Figure 29D).

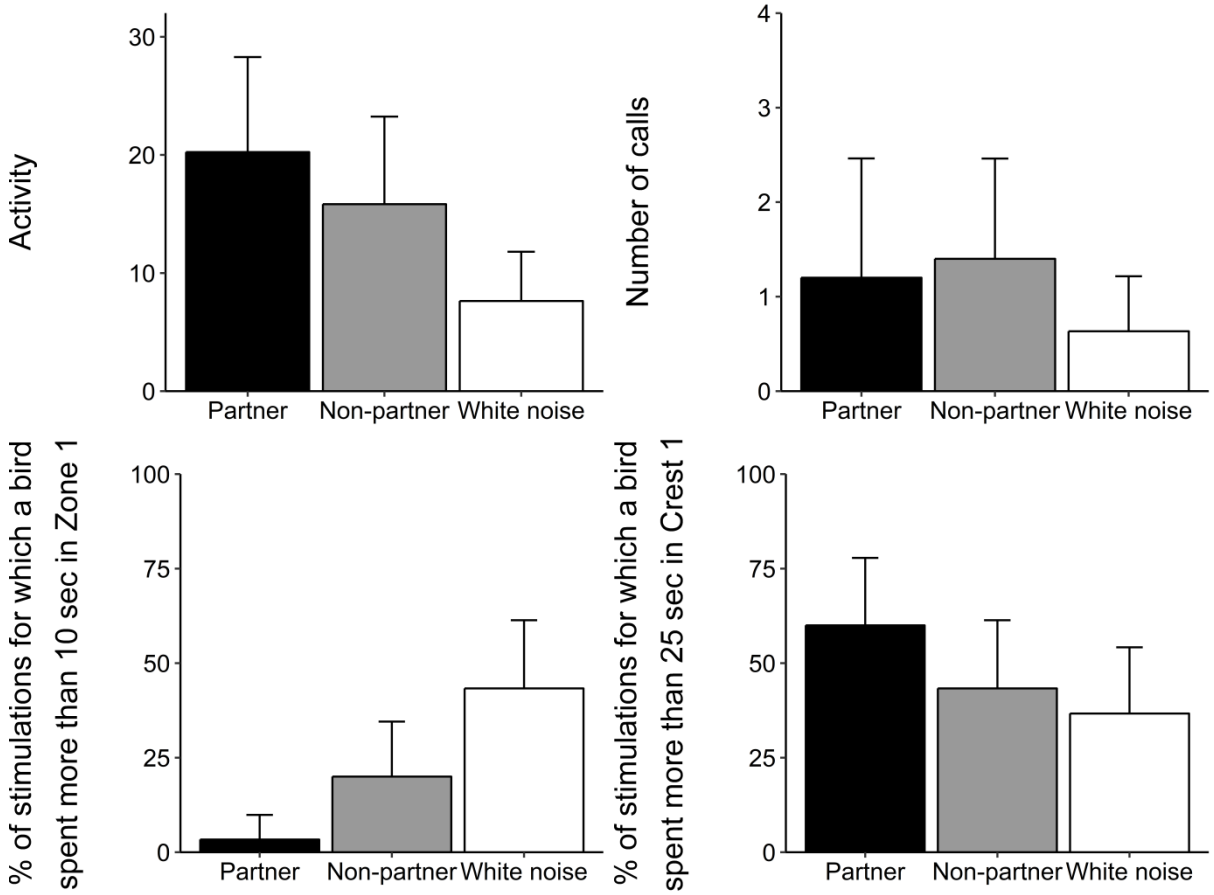

Figure 29. **Least square means ± SE. of (A) activity i.e. the number of zone changes by the subject, (B) number of calls, (C) Percentage (%) of audio stimulations for which the subject spent more than 10 seconds near the loudspeakerand (D) Percentage (%) of audio stimulations for which the subject spent more than 25 seconds in crest 1during the playback stimuli.** Statistical differences between conditions (partner, non-partner, white noise) are given (*** = $p < 0.001$; **= $p < 0.01$; *= $p < 0.05$). (A)Activity: partner 20.23 ± 4.11, non-partner 15.83 ±3.78, white noise 7.63 ± 2.13. (B)Calls: partner 1.2 ±0.64, non-partner 1.4 ± 0.54, white noise 0.63 ± 0.30. (C) Zone: partner 3.33 ±3.33, non-partner 20 ±7.43, white noise 43.33± 9.20; (D) Crest: partner 60 ± 9.10, non-partner 43.3 ± 9.20, white noise 36.67 ± 8.95.

After playback stimuli

It appears that the birds continued to react to some extent after the playback stimuli. The cockatiels continued to be more active and changed between the zones more often after playback of distress calls than after playback of white noise (partner – white noise: estimate = -1.67 ± 0.33, z = -5.06, $p < 0.0001$, $\varphi = 1.99$; non-partner – white noise: Tukey test, $p < 0.0001$). However, no difference in activity was found between the phases after partner or non-partner distress call playback (estimate = -0.34 ± 0.23, z = -1.48, $p = 0.14$).

Similarly no difference was found in the number of calls emitted after playback of a partner's or a non-partner's distress calls (estimate = -0.30 ± 0.72, z = -0.41, $p = 0.68$, $\varphi = 0.66$). As no call were emitted after playback of white noise, it was not possible to test for differences between the number of calls emitted after distress call playback or white noise playback.

The type of playback stimuli had an impact on the birds' presence near the loudspeaker. Indeed, they spent less time in zone 1 after playback of distress calls than after playback of white noise (partner – white noise: estimate = 2.22 ± 0.82, z = 2.69, $p = 0.007$, $\varphi = 0.91$; non-partner – white noise: Tukey test, $p = 0.04$). No significant difference was found in the time spent near the loudspeaker after the playback of neither partner nor non-partner distress calls (estimate = 0.28 ± 0.80, z = 0.35, $p = 0.73$).

Finally, there was no difference in time spent by the birds with a crest position 1 after playback of partner distress calls, non-partner distress calls or white noise (partner – non-partner: estimate = -0.87 ± 0.10, z = -0.87, $p = 0.38$, $\varphi = 0.67$; partner – white noise: estimate = -0.66 ± 1.12, z = -0.59, $p = 0.56$; non-partner – white noise: Tukey test, $p = 0.98$).

2. Other effects on birds' behaviours

The subjects' sex has no significant effect on any variable although there was a weak tendency for males to be more active than females when all phases were analyzed together

(estimate = 2.24 ± 1.56, z = 1.44, p = 0.15, φ = 2.52), as well as during (estimate = 2.04 ± 1.40, z = 1.46, p = 0.14, φ = 2.05) and after playback stimuli (estimate = 3.09 ± 2.00, z = 1.54, p = 0.12, φ = 1.99). The only bird that was active before audio stimulation was a female (Callisto).

There were important individual differences between birds as indicated by the high variance observed for the bird identity random effect during playback stimulation (activity, variance = 2.05; number of calls, variance = 4.87; zone 1, variance = 9.06; crest 1, variance = 16.99) and after audio stimulation (activity, variance = 4.19; number of calls, variance = 1.61; zone 1, variance = 1.12; crest 1, variance = 40.47).

Study 3: Testing prosociality in an experimental task with psittacids

Experiment 1: Other-regarding preferences in psittacids

An average of ten to thirteen sessions was needed for the birds to reach the criterion of less than two "no reward" items chosen in three successive sessions of 10 trials.

Firstly, we observed the general results with individual choices pooled together (Figures 30 & 31) and then we analyzed each bird individual preferences in order to bring to light the individual strategies and personal variability (Figures 32 & 33).

When results obtained from African grey parrots' results were pooled (Figure 30), the item chosen by the subject had a significant effect (F (2, 24) = 15.49, p =.013): African grey parrots chose more the own reward" item than the "no reward" item (p < .05) and they chose more the "both reward" item than the "no reward" item (p <.05). There is no significant difference between the "own reward" item and the "both reward" item (p =.86). The set of object (the replication of each test) also had a significant effect: "set 1" vs "set 2", "set 2" vs "set 3" and "set 1" vs "set 2", p < .05. Birds exhibited significantly different strategies depending on the replication of the experiment. However, there are no significant differences for the factor "item" within each set or for the factor "set" within each type of item (p > .05).

When conures and macaws' results are pooled together (Figure 31), we observe the same kind of results as with African grey parrots: there is a significant effect of the item (F (2, 42) = 13.96, p <.01). There is a significant difference between "own reward" and "no reward" items (p < .05); but also between "both reward" and "no reward" (p < .05). However, there are no significant differences between "own reward" and "both reward" items (p = 0.36), but we can observe a significant effect of the set of object ("set 1" vs "set 2", "set 2" vs "set 3" and "set 1" vs "set2", p <.001). We also can observe significant differences for the factor "item within

set": In set 1, there is more "own reward" items than "no reward items chosen (p = .005). In set 2, there is more "own reward" item than "no reward" items chosen (p <.001) and more "own reward" items than "both reward" items ones (p <.001). In set 3, there is more "both reward" item than "own reward" ones (p <.001) and more "both reward" items than "no reward" ones (p <.001).

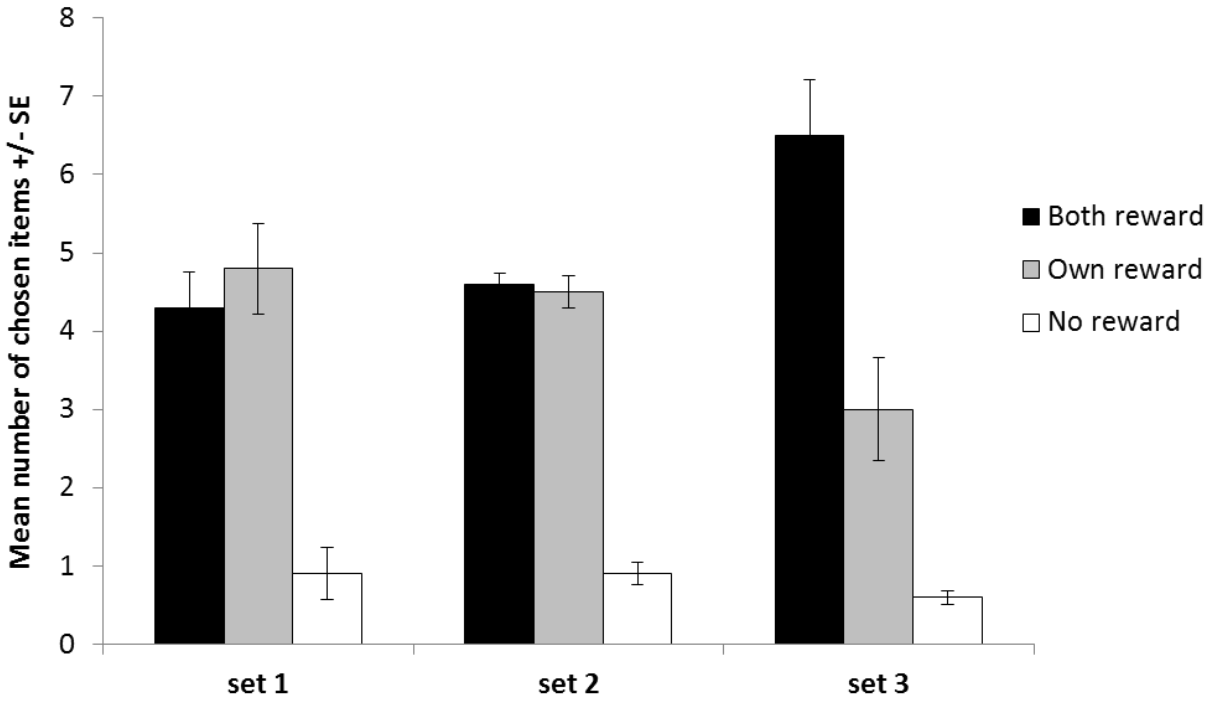

Figure 30. Mean number of African grey parrots' choices across experiment 1 with all birds pooled together (with the 3 sets of items).Two-Way RM Anova + Holm-Sidak test.

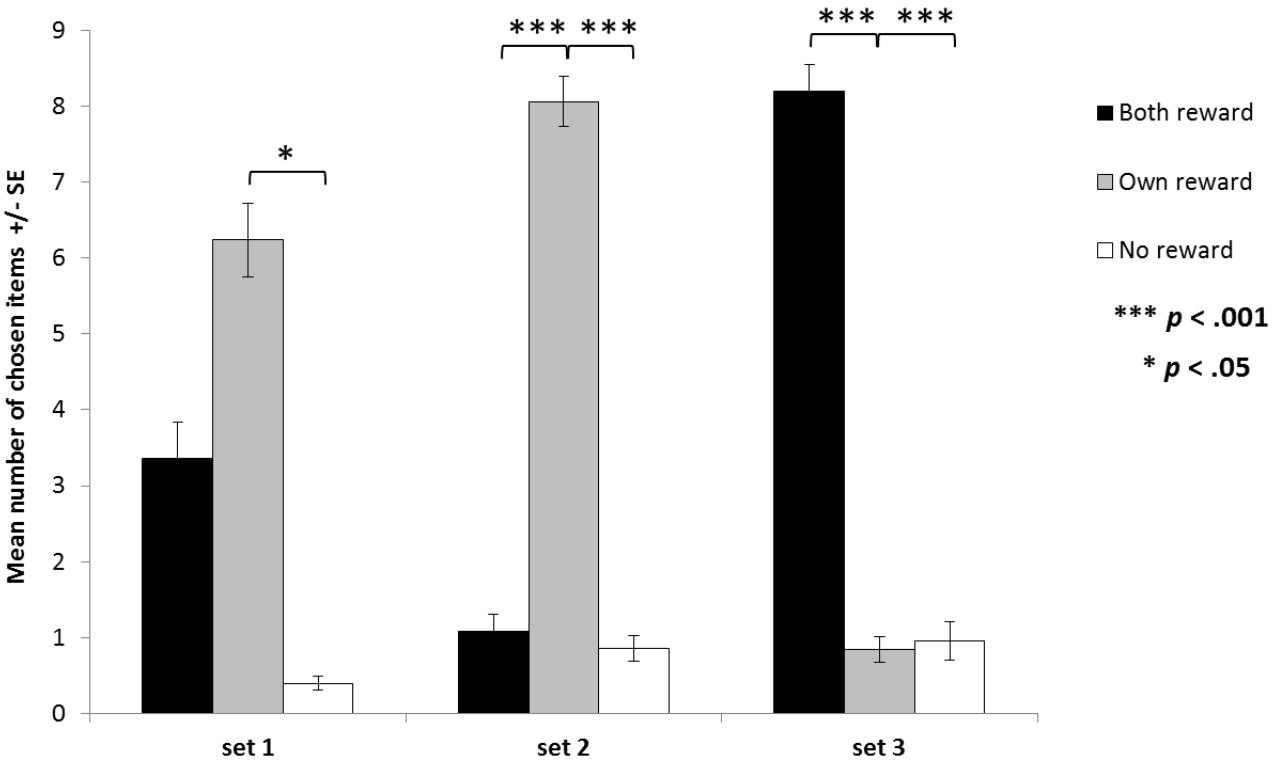

Figure 31. Mean number of conures and macaws' choices across experiment 1 with all birds pooled together (with the 3 sets of items). Two-Way RM Anova+ Holm-Sidak test, ***: $p < .001$

When we look at individual strategies, we observe that most of the subjects developed a significant preference for the "own reward" or "both reward" objects. Nonetheless, their preferences changed across the repetitions (Table 7). Sometimes the birds choose between both objects at random, especially with the first set.

Most of the birds (six out of the eight birds tested as subjects) developed a preference for the "both reward" object, with the last set of objects. We observed also that birds' preferences tended to be similar within a dyad even if it was not possible to observe any direct reciprocity.

Birds	Sex	Relation	Set 1	Set 2	Set 3
Psittacus erithacus (Zoé)	Female	Living together	**O-B**	**O-B**	**O**
Psittacus erithacus (Léo)	Male	Living together	**O-B**	**O-B**	**B**
Psittacus erithacus (Shango)	Male	Living together	**O-B-N**	**O**	**B**
Ara glaucogularis	Female	Mated pair	**O**	**O**	**B**
Ara glaucogularis	Male	Mated pair	**O**	**O**	**B**
Aratinga solstitialis (MUG)	Male	Sibling	**O**	**O**	**B**
Aratinga solstitialis (BG)	Male	Sibling	**B**	**O**	**B**
Ara macao	Male	Mated pair	**B**	**O-B-N**	**B-N**

Table 7. Individual choices of all birds in experiment 1with the 3 sets of items. Analyses were done on the ten last sessions per set per bird (Friedman RM Anova on ranks + Tukey test). O: "Own reward" item; B: "Both reward" item; N: "No reward" item. **O-B-N:** no significant $p > .05$; **O-B** or **B-N**: significant difference with the third alternative; $p < .05$; **O** or **B**: significant difference with the two other available choices; $p < .05$

African grey parrots

The grey parrots were tested with two different partners but no difference in the behaviour of the subject according to the partner identity was found. We observed that each individual adopted a strategy at the end of the experiment (set 3): Zoé chose more often the "own reward" item than the two other items and Léo and Shango, the two males, showed a preference for the "both reward" item (Figure 32).

Shango and Zoé emitted frustration calls after the subject made his decision. For Zoé, these calls were produced significantly more often when her partner chose the selfish object compared to the two others (Chi-Square test, χ 2 (2, N = 10) = 12.22, $p < .001$).

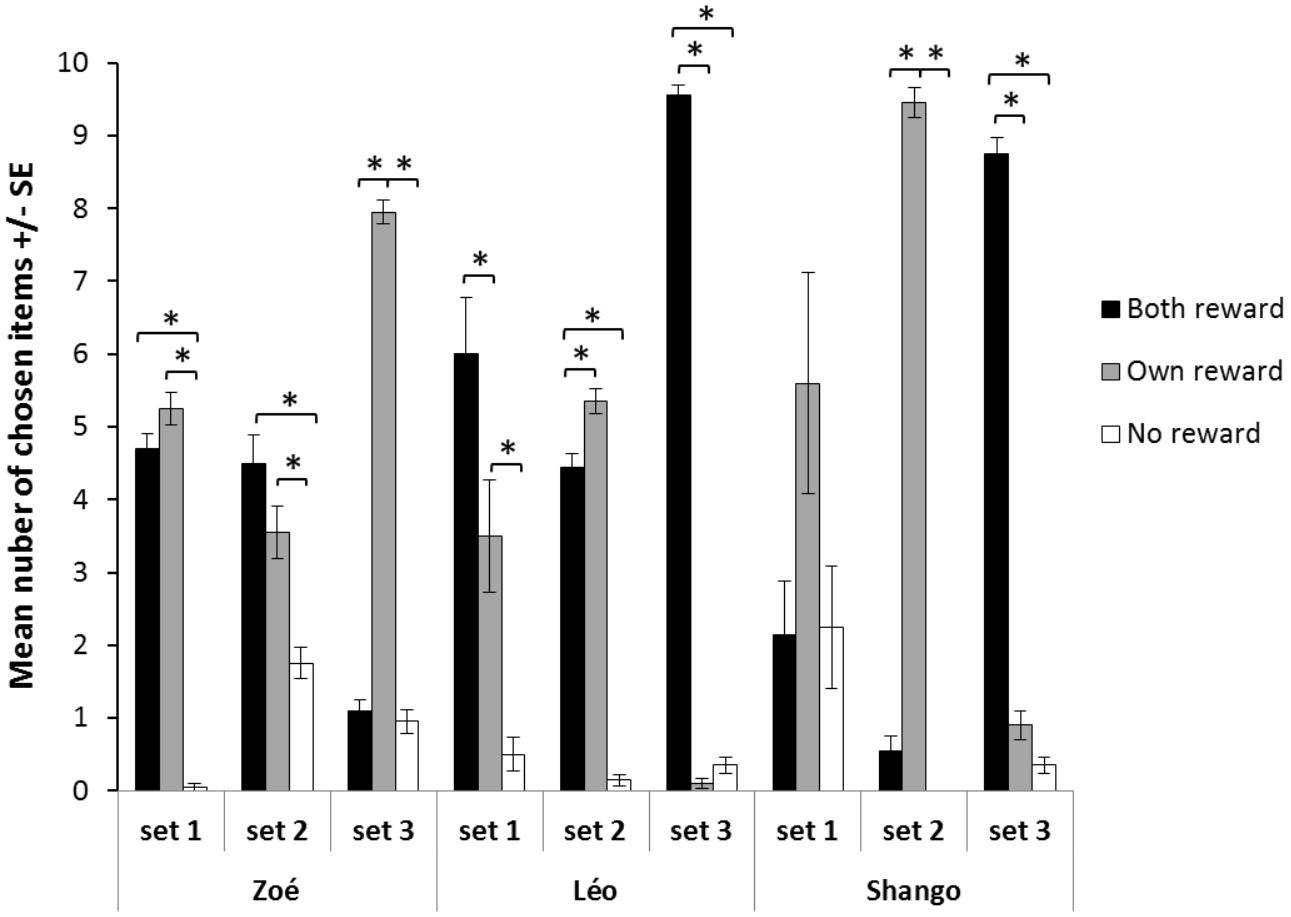

Figure 32. Mean number of African grey parrots' individual choices across experiment 1 (with the 3 sets of items). Friedman RM Anova on ranks + Tukey test; *: $p < .05$

Other parrots

The female *A. macao* refused to interact with the objects; therefore, only the male was tested because his female accepted to come and take the reward nevertheless. However, this male kept choosing between the objects at random, and picked the "no reward" item even at the end of experiment, with the third set of items. Due to this unusual choice, it was not possible to conclude whether he really understood the task. Other individuals chose preferentially the "own reward" option with the first set of objects and changed their preference to the "both reward" option with the third set. In the end, four out of five birds chose preferentially the "both reward" object with the last set of objects (Figure 33). Contrary to African grey parrots, macaws and conures did not vocalize during the exchanges so we cannot conclude about their frustration and emotional state.

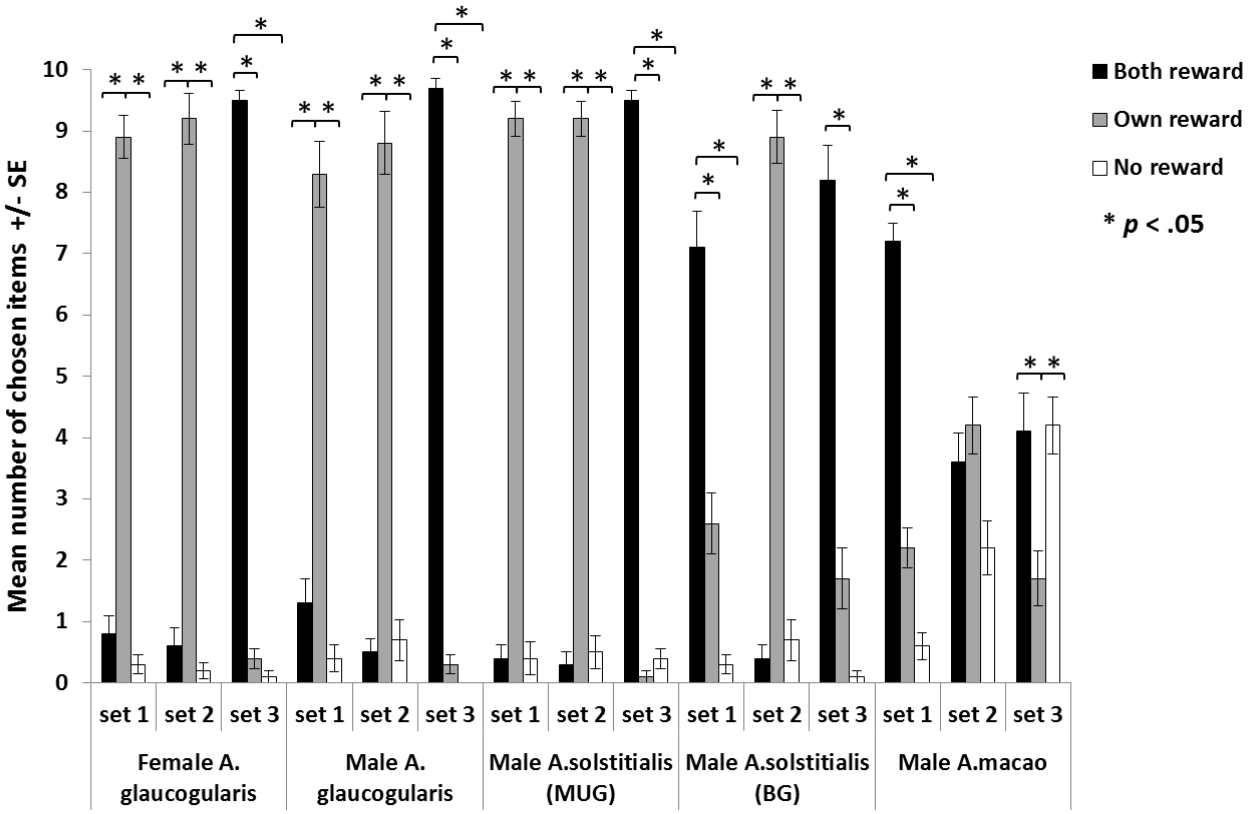

Figure 33. Mean number of macaws and conures' individual choices across experiment 1 (with the 3 sets of items). Friedman RM Anova on ranks + Tukey test; *: $p < .05$

Most individuals anticipated the fact to be rewarded: they approached the experimenter when the tested bird chose the “both reward” object (Table 8). A comparison on proportions of the number of anticipation events divided by the items chosen by the subject, for every type of item for all individuals produced the following results : there is a significant difference between the three type of items chosen (F (2,7) = 11.036, p <.001). The number of anticipated rewards by the partner when the subject chose the “both reward” object is significantly different from the two other conditions: birds anticipated more the reward when the subject chose the “both reward” item compared to the “no reward” one (p <.01) and when they chose the “both reward” item compared to the “own reward” item (p <.01) whereas no significant difference was found between “no reward” and “own reward” conditions (p = .89).

		Reward anticipation by the partner			**Items chosen by the subject**			
Subject	**Partner**	**Both reward**	**Own reward**	**No reward**	Both reward	Own reward	No reward	Total
Males *P. erithacus* (Shango + Léo)	Female *P. erithacus* (Zoé)	**12**	**2**	**0**	151	139	10	300
P. erithacus (Shango + Zoé)	Male *P. erithacus* (Léo)	**6**	**1**	**0**	105	163	32	300
P. erithacus (Léo + Zoé)	Male *P. erithacus* (Shango)	**1**	**0**	**0**	145	134	21	300
Male A. glaucogularis	Female *A. glaucogularis*	**60**	**1**	**0**	115	174	11	300
Female A. glaucogularis	Male *A. glaucogularis*	**91**	**2**	**0**	109	185	6	300
Male *A. solstitialis* (MUG)	Male *A. solstitialis* (BG)	**72**	**0**	**0**	102	185	13	300
Male *A. solstitialis* (BG)	Male *A. solstitialis (*MUG)	**79**	**0**	**0**	157	132	11	300
Male *A. Macao*	Female *A. macao*	**45**	**5**	**0**	149	81	70	300

Table 8. Number of reward anticipations (i.e., approaches of the experimenter) by the partner during experiment 1 depending on the item chosen by the subject. The results show all anticipations events observed with the 3 sets of items per bird.

Experiment 2: Influence of inequity on other regarding-preferences

When we pooled all birds' choices together (Figure 34), we did not observe any significant effect of the condition (inequity vs control) ($F(1, 15) = 16.33$, $p = 0.056$) and the item ($F(2, 15) = 1.79$, $p = 0.28$). Moreover, we observed a significant difference for the interactions between "condition" and "item" ($F(2, 15) = 12.84$, $p = 0.018$): there was more "both reward" items chosen in inequity condition than in control condition when all birds were pooled together ($p < .001$). Nevertheless, when we focussed on individual strategies, we observed that African grey parrots kept the same strategy as during the last repetition of the first experiment. Also some important inter-individual variability in strategies appeared between birds (Figure 35).

Indeed, in control condition, Zoé kept choosing more often the "own reward" object (Median = 7.5) than the "both reward" object (Median = 1) and than the "no reward object (Median = 0.5) ($\chi 2 (2, N = 8) = 13.31$, $p < .001$). The Tukey test revealed that, in control condition, Zoé chose more often the "own reward" item than the "no reward item" ($p < 0.05$) and than the "both reward" one ($p < 0.05$). In the inequity condition there was no significant difference between item choices ($\chi 2 (2, N = 8) = 5.60$, $p = .08$).

Contrary to Zoé, the female, males kept choosing the "both reward" item most of the time. In both conditions, Léo chose more the "both reward" item than the two others objects. In control conditions, we obtained the following results for "both reward" (Median = 10), "own-reward" (Median = 0) and "no-reward" items (Median = 0) ($\chi 2 (2, N = 8) = 13.71$, $p = .001$). The Tukey test revealed that in control condition, Léo chose more often the "both reward" item than the "own reward" item ($p < .05$) and than the "no reward" item ($p < .05$) A similar pattern is observed in inequity condition ($\chi 2 (2, N = 9) = 17.43$, $p < .001$): Léo chose more

the “both reward” item than the “own reward” item($p < .05$) and than the “no reward” item ($p < 0.05$).

In control condition, Shango chose more the “both reward” item (Median = 9.5) than the “no reward” item (Median = 0) (χ 2 (2, N = 7) = 11.14, p =.002) but there was no significant difference for the other comparisons. In inequity condition, Shango obtained the following results for “both reward” item (Median = 10),“own reward” item (Median = 0) and “no reward” item (Median = 0) (χ 2 (2, N = 8) = 14.30, $p < .001$). The Tukey test revealed that in inequity condition Shango chose more the “both reward” item than the “own reward” item ($p < .05$) and than the “no reward” item (p <.05). There was no significant difference between “own reward” and “no reward” items in inequity condition (p >0.05).

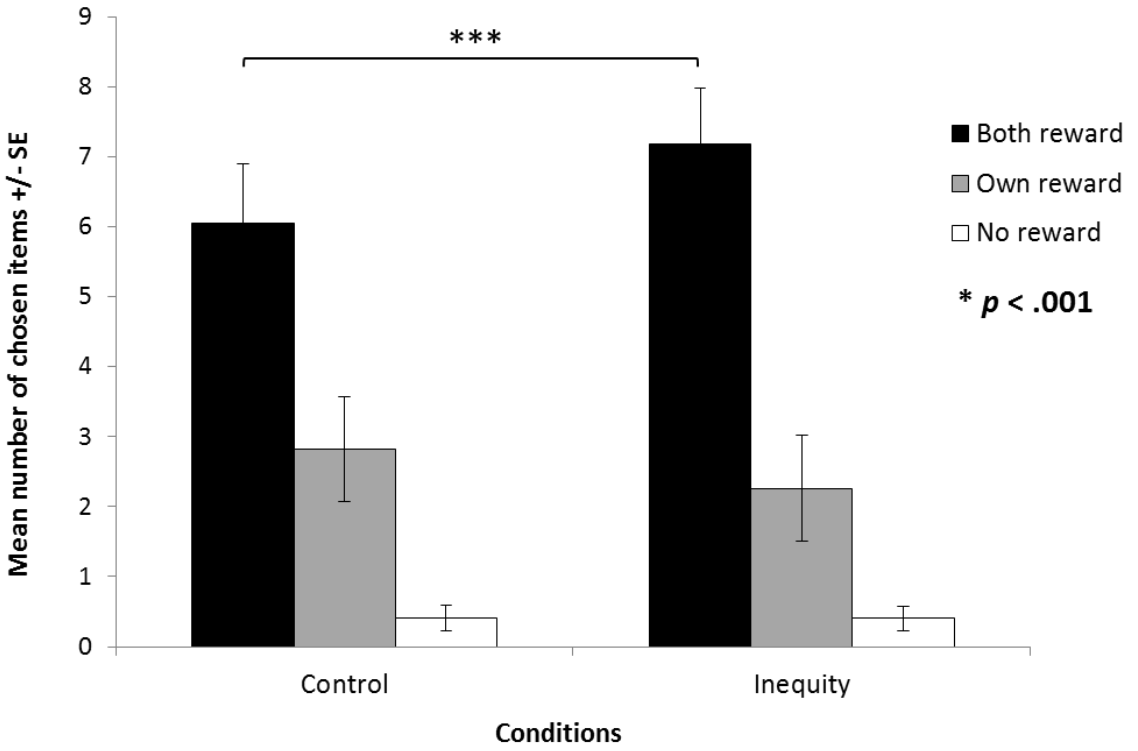

Figure 34. Mean number of African grey parrots’ choices in control and inequity conditions with all birds pooled together (experiment 2). Two-Way RM Anova+ Holm-Sidak test, ***: p <.001

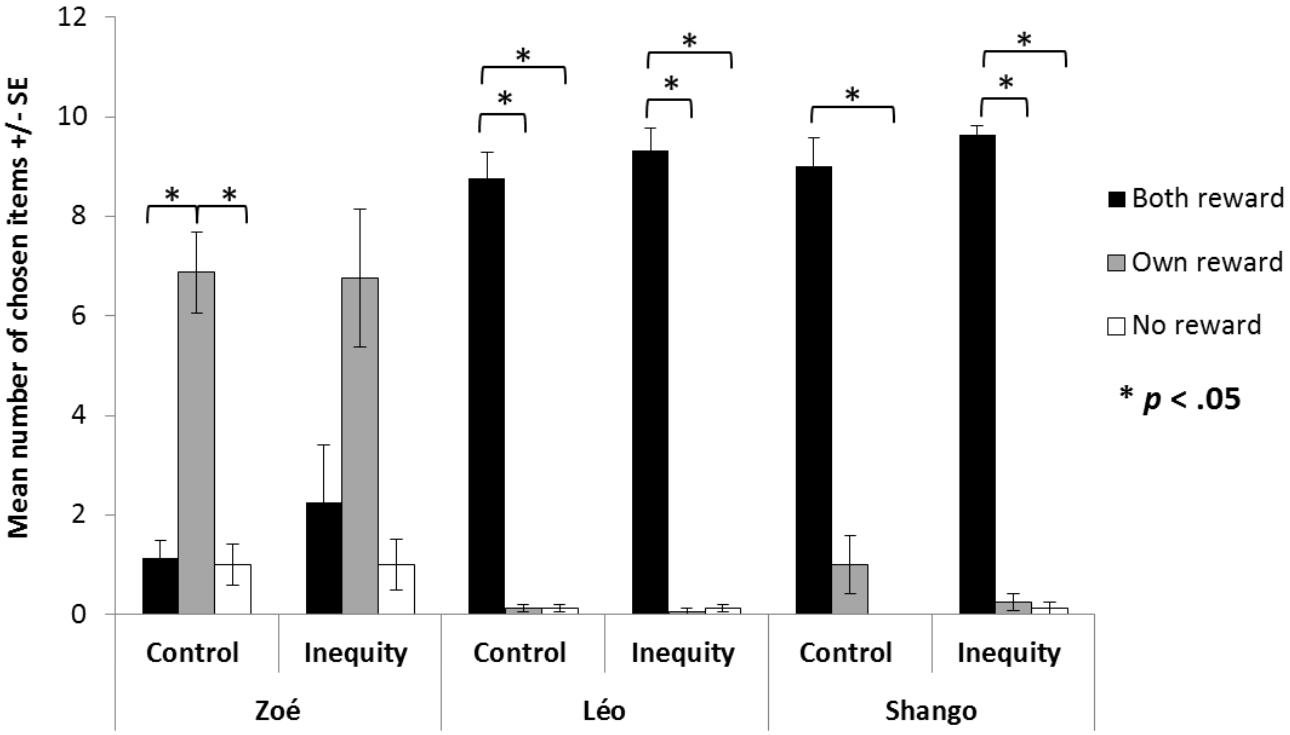

Figure 35. Mean number of African grey parrots' individual choices in control and inequity conditions (experiment 2). Friedman RM Anova on ranks + Tukey test; *: p <.05

Experiment 3: Influence of other regarding preferences on the maintenance of cooperative behaviour

During this third experiment, Léo obtained the following results for "both reward" item (Median = 5) "own reward" item (Median = 4) and "no reward" one (Median =0 (χ 2 (2, N = 23) = 35.54, p < .001). The Tukey test revealed that there was more "both reward" items chosen compared to "no reward items (p<.05) and more "own reward" item compared to "no reward" item (p <.05). But there was no preferences between the "both reward" item and the own reward" item (p > .05) (Figure 36).

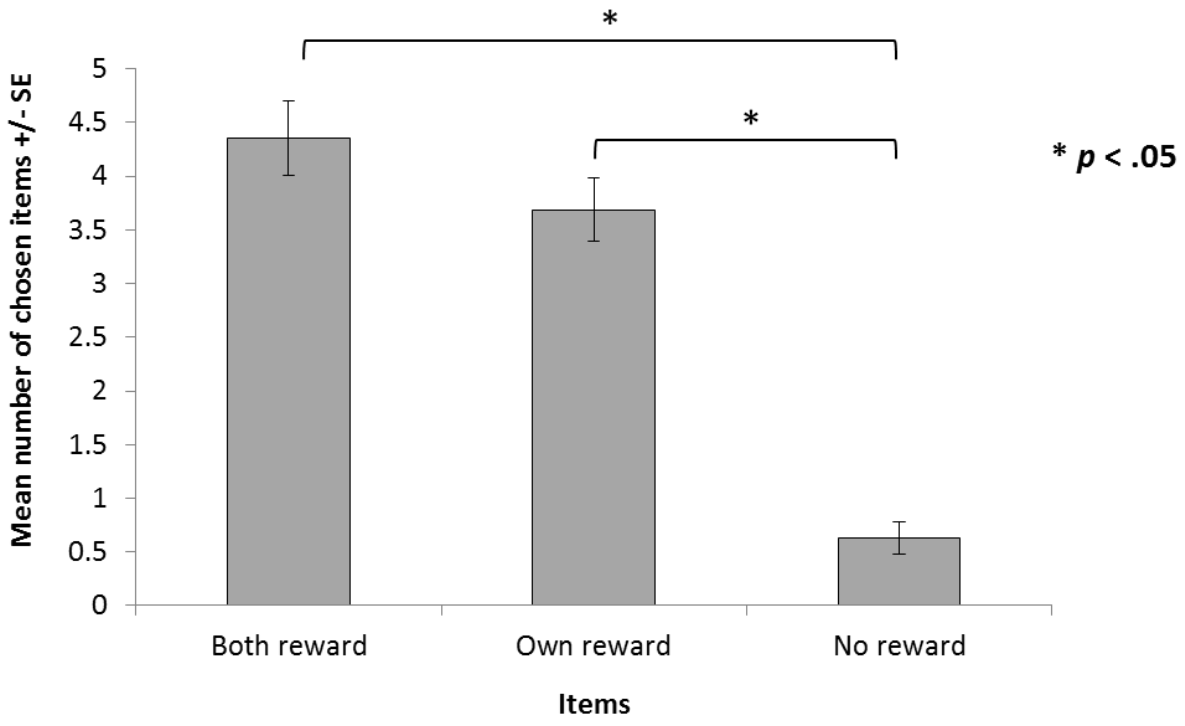

Figure 36. Mean number of Léo's choices (the subject) in experiment 3. Friedman RM Anova on ranks + Tukey test; *: p <.05

Shango acted differently depending on the item he received from Léo (Two-sided Fisher exact test, $p < .001$): There are more "both reward" items transferred (105/114) than "own reward" (47/99) and "no reward" items (5/12) (see Figure 37). There are significant differences between "both reward" and "own reward" ($p < .001$) and between "both reward" and "no reward" ($p < .05$) but no differences between "own reward" and "no reward" items ($p = 1$).

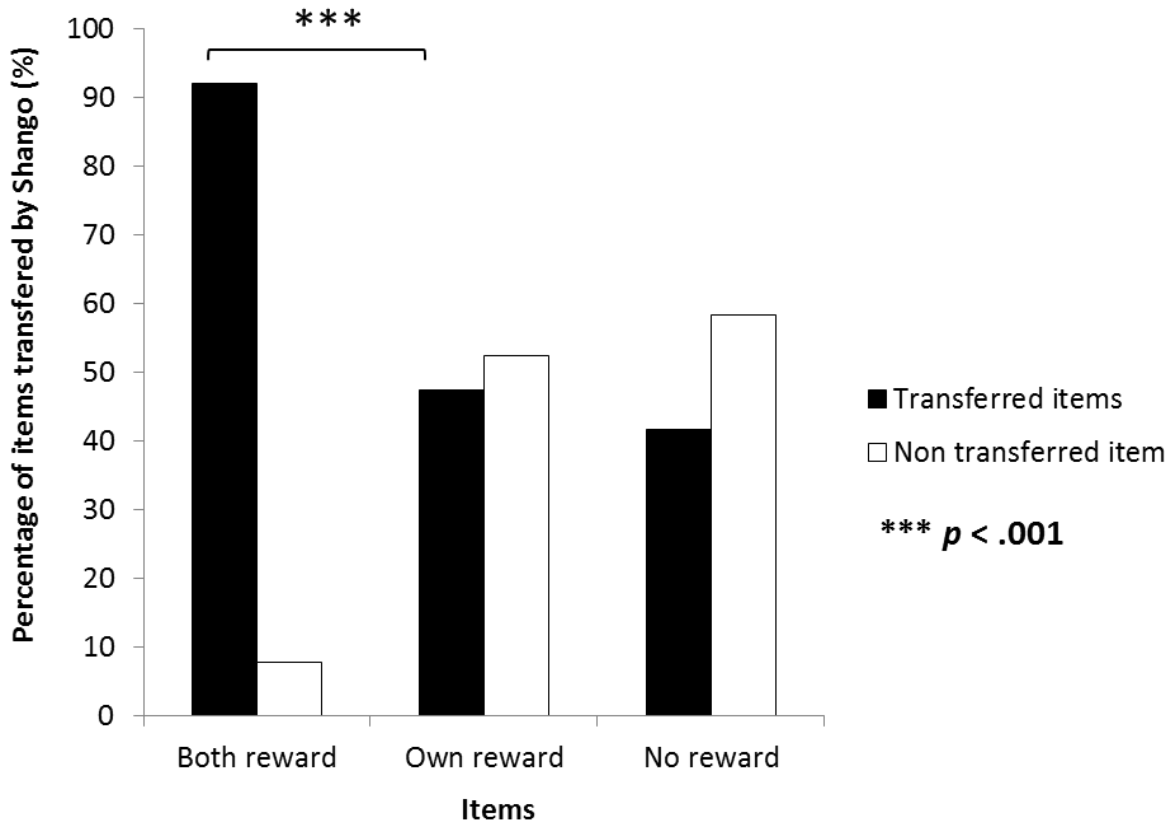

Figure 37. Percentage of items transferred by Shango (the receiver) according to the object received from Léo during experiment 3. Fisher exact test, ***: p <.001

Moreover, Shango reacted differently depending on the item he received from Léo. Concerning frustration, Shango expressed more behaviours such as cardboard biting, beak scraping and frustration calls, when Léo chose the "own reward" (21/99) item compared to the "both reward" (4/114) item (Two-sided Fisher exact test, p < .001). He also left the apparatus and flew away more often when Léo chose the "own reward" item (32/99) compared to the "both reward" item (9/114) (Two sided Fisher exact test, p < .001) (see Figure 38). Also, Shango threw the "own reward" item (14/99) out of the table more often than the "both reward" item (2/114) (Two-sided Fisher exact test, p = .001).

The number of "own reward" items transferred by Shango decreased over time (Spearman correlation, N = 22, r_s = - 0.701, p < .001).

We also observed some anecdotal aggressive displays from Shango towards Léo when he failed to transfer any item. However they have been too rare to be statistically significant.

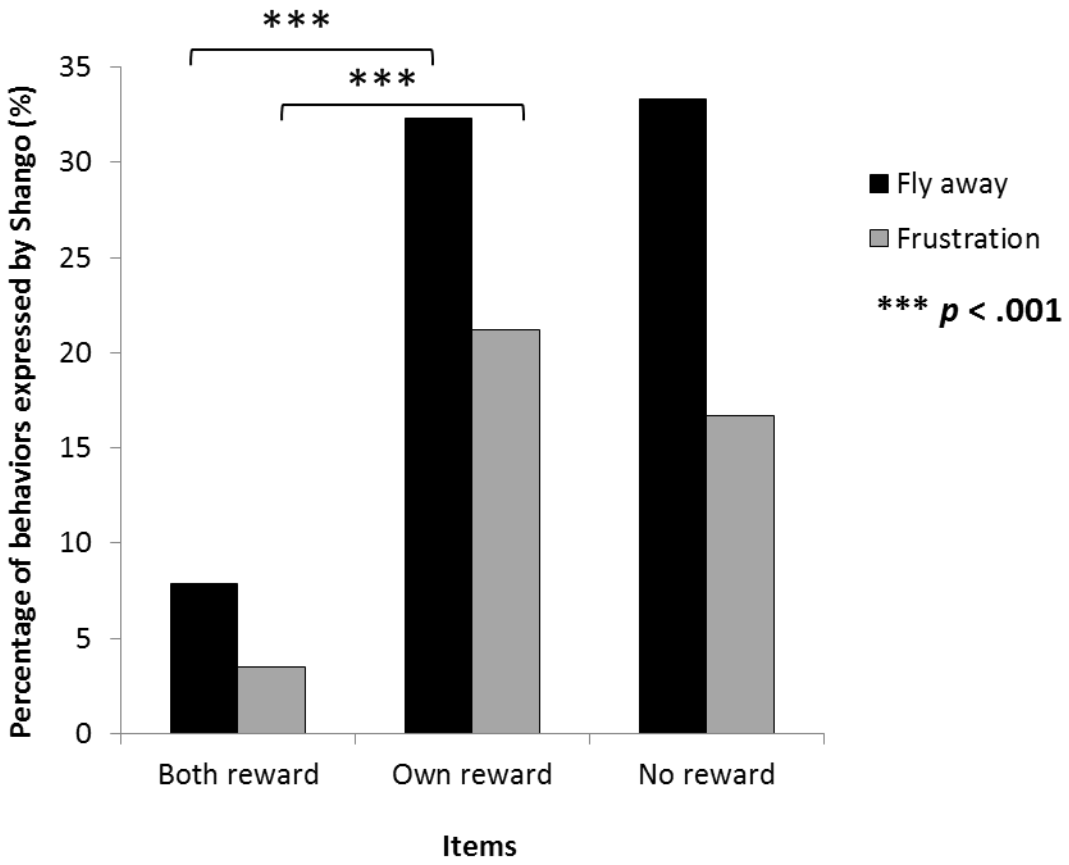

Figure 38. Percentage of Shango's behaviours (frustration and flying away) according to the object received from Léo during experiment 3. "Frustration" includes cardboard biting, beak scraping and frustration calls. Fisher exact test, ***: p <.001

Study 4: Impact of social contexts on novel object exporation in jackdaws

Proximity and aggressive behaviors

There was a significant effect of the interaction between the condition (partner or non-partner) and the situation (intimidating or not) on the number of proximity events within a dyad (interaction condition X situation: X_1^2 = 7.450, p = 0.006). Hence, number of proximity events within a partner dyad was higher in a scary situation (1.97±0.59 proximity events per test) than in a non-scary situation (1.50±0.51) whereas it was the opposite for non-partner dyads (scary: 1.23±0.39; non-scary: 2.44±0.63). Regarding the number of aggressive displays, there was no effect of the interactions or the situation or the sex (all $p > 0.135$).

However, birds displayed more aggressive behaviors toward their non-partner than toward their partner during the tests (partner: 0.41±0.13 aggressive displays per test; non-partner: 0.66±0.17; X_1^2 = 6.125, p = 0.013).

PCA

PC1 captured variation linked to all the four variables and explained 70.5% of variation observed in the sample. All variables except the number of times the birds touched the object were negatively correlated to this axis (Table 9). A high PC1 score therefore represents a bird that was quick to reach the large circle, to eat and to touch the object and that frequently touched the object.

Behaviors	PC1	PC2	PC3	PC4
Latency to reach the large circle	-0.503	-0.523	-0.185	-0.663
Latency to eat	-0.529	-0.424		0.736
Latency to touch the object	-0.510	0.400	0.749	-0.137
Frequency of contact with the object	0.455	-0.622	-0.636	

Table 9. Principal component analysis of four explorative behavioral traits. PC1, PC2, PC3 and PC4 explain, respectively, 70.5%, 20.7%, 5.8% and 2.9% of variation observed in the sample. Empty cases correspond to values below 0.1.

Probabilities

Regarding the probability to reach the large circle, there was no effect of the interactions, the condition and the sex (all $p > 0.201$). However, the more explorative birds (PC1 scores) were significantly more likely to reach the circle ($X_1^2 = 34.604$, $p < 0.001$) and all jackdaws were more likely to reach the circle in the non-intimidating situations than in the more intimidating situations (intimidating: 0.62±0.03; non-intimidating: 0.84±0.03; $X_1^2 = 18.776$, $p < 0.001$).

The same results were found regarding the probability to eat, with no effect of the interactions, the condition and the sex (all $p > 0.253$) but the more explorative subjects were more likely to eat ($X_1^2 = 32.170$, $p < 0.001$) and all jackdaws were more likely to eat in the non-intimidating situations than in the intimidating situations (intimidating: 0.53±0.03; non-intimidating: 0.82±0.04; $X_1^2 = 23.586$, $p < 0.001$).

Regarding the probability to touch the object, the interaction between the condition and the explorative rank was not far from being significant (X_2^2 = 5.265, p = 0.071). More explorative birds tended to be more likely to touch the object when alone than when with another bird whereas less explorative birds were more likely to touch the object when with a non-partner bird than when tested with their partner or alone. Other fixed effects were not significant even if there was a tendency for birds to be more likely to touch the object in the non-intimidating situations (0.42±0.07) than in the intimidating situations (0.25±0.03; X_1^2 = 3.199, p = 0.074).

The probability to remove the object was higher for males (0.15±0.03) than for females (0.09±0.03; X_1^2 = 3.974, p = 0.046). More explorative birds were also more likely to remove the object (X_1^2 = 17.036, p < 0.001). Interactions were not tested because convergence failed when they were included. Other terms were not significant (all p > 0.091). The "schematic eyes" category was not included in the analysis because birds never removed this object.

Latencies

Regarding the latency to reach the large circle, there was a significant interaction between the condition and the explorative rank (X_2^2. =6.712, p = 0.035)

Less explorative birds were quicker to reach the circle when tested with their partner than when tested with another bird or alone but there was no effect of the condition for the more explorative birds, which were not influenced by the presence of a partner and reach the circle at the average same speed (Figure 39). The birds were also quicker to reach the circle in the non-intimidating situations (53.2±13.7 seconds) than in the intimidating ones (95.9±17.2 sec; X_1^2 = 4.621, p = 0.031) and males (59.2±14.3) reach it faster than females (95.2±17.9 sec;

X_2^2 = 6.227, p = 0.048). Others terms were not significant (all p > 0.091). There was a significant effect of interaction between the condition and the sex on the latency to eat (X_2^2 = 6.100, p = 0.047) (Figure 40). Females were slower to start eating when alone (145.3±38.3 sec) than when with their partner (66.1±18.5 sec) or another bird (91.0±37.7 sec) whereas there was no such extreme differences between conditions for males (alone: 67.3±26.5 sec; partner: 43.3±12.2 sec; non-partner: 58.1±31.1 sec; Figure 40).

Birds were also slower in the intimidating situations (94.3±18.7 sec) than in the non-intimidating situations (64.9±15.2 sec; X_1^2 = 10.278, p = 0.001) and more explorative jackdaws were quicker to start eating (X_1^2 = 8.912, p = 0.003). Other terms were not significant (all p > 0.225).

Regarding the latency to touch the object, only the sex effect was significant (X_1^2 = 4.880, p = 0.027) with females (176.3±31.2 sec) being slower than males (111.6±37.5 sec). Other terms were not significant (all p > 0.217).

The model looking at effects on the latency to remove the object did not converge probably because it was a rare event (27/279 tests).

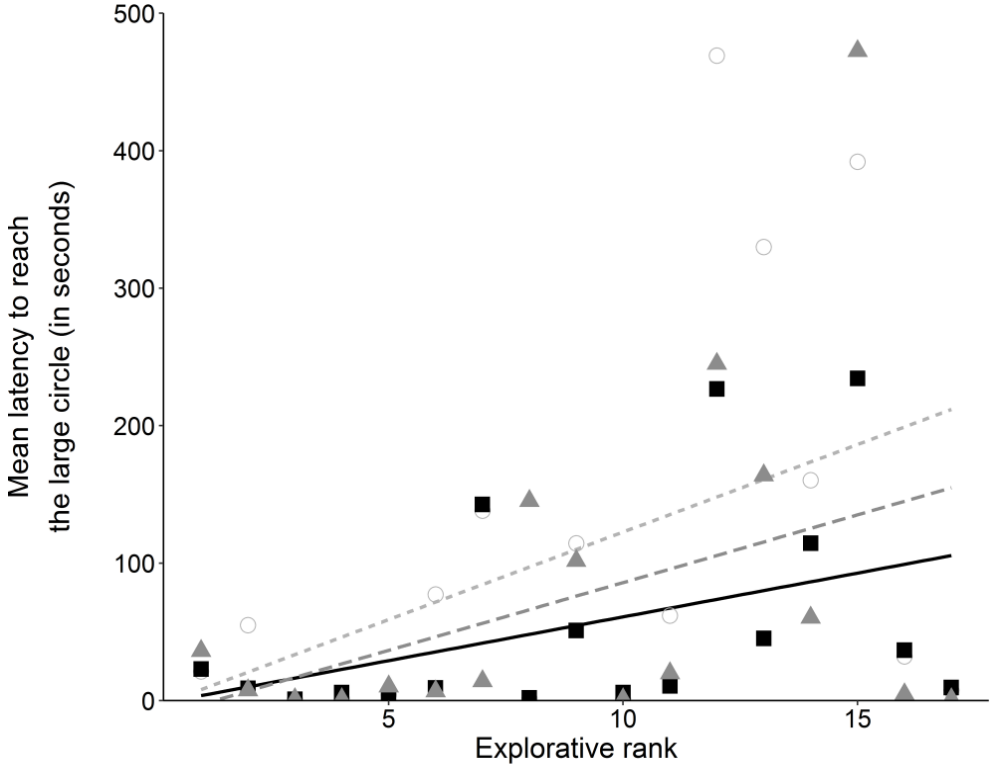

Figure 39. Mean latency to reach the large circle in seconds when the jackdaws were tested with a partner (■), with a non-partner (▲) and alone (○) depending on the explorative rank.

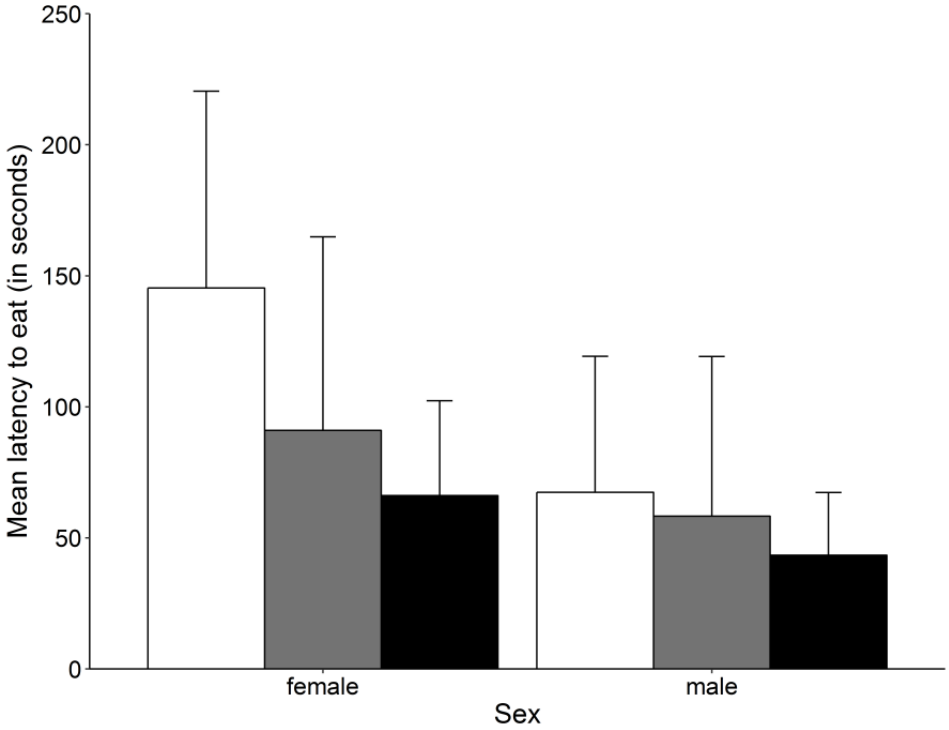

Figure 40. Mean latency to eat in seconds when the jackdaws were tested alone (white column), with a non-partner (grey column) and with their mate (black column) in female and male. Histograms are presented with the standard errors.

Discussion

Discussion

The aim of this thesis was to investigate the implication of social relationships and affiliation in prosociality and empathy in two species of birds, cockatiels and jackdaws, respectively from psittacids and corvids families. The main hypothesis was that prosociality was enhanced between preferred partners, which are also potentially sharing emotional bonds. It is indeed suggested that empathy, especially between siblings, mates and affiliated birds ("friends"), will drive prosociality as suggested by Decety et al (2016). Psittacids and corvids are especially renowned for their specific mating association involving long-term monogamy. This type of association has been defined as cognitively demanding and could be one of the selective pressure for the emergence of intelligence in these birds (Emery, Seed, von Bayern, & Clayton, 2007). Indeed this social complexity between partners implies cooperation during and outside breeding season but also to keep tracks of past interactions with others. Some of these birds have even demonstrated abilities involving Theory Of Mind-like abilities in some corvids species via food-caching experiments (Dally, Emery, & Clayton, 2006) and food-sharing paradigm (Ostojić, Shaw, Cheke, & Clayton, 2013), suggesting they are able to take the other's mental states into account. Furthermore, empathy does not require complex cognitive capacities such as theory of mind or conscious awareness of others' feelings, but it implies a discrimination between the self and the others (Decety et al., 2016) (Bischof-Köhler, 2012). Consequently, empathy could exist between preferred partners and could be one of the main drivers of prosociality. The complex link between affiliation, empathy and prosociality still remains to be explored further.

1) Testing prosociality in parrots and corvids

In this thesis I investigated prosociality with different species and through different types of paradigms, using both artificial experimental tasks and more natural settings to study spontaneous behaviors like food sharing.

Both cockatiels in the first study and psittacids tested in the third study showed prosocial tendencies: parrots were tested via an artificial task (the exchange of tokens) and cockatiels via a more natural task (food-sharing). Nevertheless, the two tasks presented some major differences: the food-sharing experiment was evaluating a spontaneous behavior while the sharing of resources in the PCT experiment was forced by a human experimenter and birds had to understand the values of tokens to obtain a reward. The task in experimental condition was more controlled but was also more artificial. Moreover, in the food sharing experiment, letting the piece of food goes to another individual represented a cost while in the PCT paradigm, there was no cost at rewarding a partner, because the subject received a reward when he chose both selfish and prosocial options ("own reward" and "both reward" tokens). Consequently, both experiments were complementary and evaluated different aspects of prosociality. Now, the best option to better understand prosociality in these two species would be to use the same paradigm.

Unfortunately, both cockatiels and jackdaws failed to show prosocial tendencies when tested with the same paradigm. Both have been tested with an experimental set-up involving the opening of boxes to deliver (or not) food to their partners. The paradigm was adapted from Schwab et al (2012) (See Appendix I). However, these observations were not sufficient to conclude about prosociality in these birds. Cockatiels were not habituated enough to the apparatuses and they did not manipulate much with their beak, contrary to other parrot species. Consequently, it is possible that the task was not adapted to this avian model. Concerning jackdaws, they understood how to use the apparatus and open boxes but did not

choose significantly more the baited box than the empty one, even though they have been tested twice a day during two months. It is likely that the design of the task involving two choices was at the origin of the failure. In corvids, some studies demonstrated that birds displayed a high level of failure in that type of task (von Bayern, 2008). We can then hypothesize that in our study, jackdaws were more motivated by the fact to manipulate and open the box than by the food reward alone.

Consequently, since many bird species are neophobic, we can then design new tasks to assess prosociality via spontaneous natural behaviors such as nest construction and defense where birds had to help each other to construct it and defend it again intruders (Röell & Bossema, 1982) or during coalition formation. Jackdaws are also known to share very strong bonds with their mate so we could also try to test rescue behavior as it was evaluated with rodents in several experiments involving restrainers (Ben-Ami Bartal, Decety, & Mason, 2011) (Ben-Ami Bartal, Rodgers, Bernardez Sarria, Decety, & Mason, 2014). This type of experiment has been tested on a short period of time with cockatiels (see Appendix I) but unfortunately they did not received enough training sessions with the box to observe conclusive resultson their ability to solve the task. Since jackdaws are more habituated to manipulate with their beak I think they may easily learn how to free a partner and they may be probalby highly motivated to help their sexual partners to escape.

a) Food sharing in cockatiels

In the first study, we investigated how affiliation and social relationships modulated food sharing in cockatiels over a 3 years longitudinal study. This study shows four main results. First, young cockatiels shared food with several different individuals although the number of recipients as well as the number of food transfers (cofeeding and stealing) noticeably decreased over their first three years of life. Second, the cockatiels transferred more food to their siblings than to unrelated birds. Third, they shared their preferred type of food more than the less preferred one. Finally, cofeeding was both reciprocated and interchanged with affiliative behavior (allopreening).

Concerning the ontogeny of food-sharing over the study period, we found a similar developmental pattern in cockatiels than in jackdaws: food sharing frequency and the number of food sharing partners decreased over time. This fast decrease in food sharing pattern over time was not observed in rooks (Scheid et al., 2008). In young jackdaws, the decrease was fast and steep, while in cockatiels, even if there was a marked decrease, birds still continued to cofeed after three years with two individuals on average. In jackdaws, the rather abrupt shift seems to be taking place roughly after 3 months post fledging when the birds are still immature (de Kort et al., 2006). When they are sexually mature, jackdaws share food exclusively with one partner, and usually in a courtship context (Wechsler, 1989), with mostly the male initiating the transfer towards the female (Kubitza et al., 2015). Consequently, it has been argued that food-sharing in juveniles may serve as an honest signal important in later mate selection, indicating potential high-quality partners (von Bayern et al., 2007). Even if the number of individuals with whom the cockatiels shared food decreased over time like in jackdaws (von Bayern et al., 2007), they still shared food with two or three different partners in their second and third year, similar to rooks (Scheid et al 2008). These contrasting results can be due to differences in sociality (Emery, 2016). Indeed, rooks not only form exclusive

pair-bonds with their sexual partners but also maintain multiple affiliative relationships when mature (Boucherie et al., 2017). As colonial breeders, rooks must be tolerant because they spend a significant amount of time in close proximity with other group members (Boucherie, 2016). In jackdaws, even if birds aggregate in colony, the tolerance between members of different pairs can be low. The pair-bond represents the strongest unit and even if all members of the colony can cooperate to mob predators, pairs exhibit high levels of competition for resources towards other members of the colony.

Moreover, a pair-bond formation explanation for cofeeding would predict more transfers between males and females. Although cockatiels and rooks shared food with several partners, they show a preference for one specific partner, and it is crucial to highlight that this preferred individual is not necessary a heterosexual partner. No sex effect was found on the cofeeding rate in cockatiels. Same-sex dyads shared as much as heterosexual dyads but no food sharing occurred between females in cockatiels. In rooks, the four females of the group received food but never offered food. Moreover no significant sex difference was found in the tendency to cofeed (Scheid et al., 2008). In primates, the literature suggests that females may be more empathic (Eisenberg & Lennon, 1983; de Waal, 2008; Christov-Moore & Iacoboni, 2016) and are more willing to share food with their offspring (Silk, 1978) than males. However, it has been observed in chimpanzees cooperative-hunters that females rarely share food with each other (Rose, 1997). Similarly, female cockatiels did not cofeed with each other and also rarely with males. They even tended to avoid contact with others during food-sharing trials.

After the last period of the food-sharing experiment, we gave birds access to nest-boxes and two mated pairs formed: Nephtys and Seth, which were siblings and shared food extensively and Hermes and Viviane, which were unrelated and only exchanged very few pieces of food at the beginning of the experiment. Even if these observations are anecdotal, they strengthen the view that food transfers are not mandatory for pair bond formation in cockatiels. In rooks

a similar pattern was found. There was no detectable sex effect in co-feeding rate, there were multiple sharing partners and no donor or preferred receiver in food-sharing interactions formed pair-bonds later in life (Scheid et al., 2008).

Our results are more consistent with the kin-selection theory (Hamilton, 1964) than with the bond formation explanation. In our group of cockatiels we found that siblings shared more food via cofeeding than unrelated birds, even when they became adults at the end of the experiment. These results are in line with those observed in rooks: birds do cofeed with their nestmates more often than expected by chance (Scheid et al., 2008). In another study on plant-food sharing by wild chimpanzees, most exchanges occurred between mother and offspring, but there were also some sharing between sibling dyads and other close relatives. In total, related dyads accounted for 86% of all food exchanges observed (McGrew, 1979). Sharing food with siblings seems to be a costly but still paying-off strategy to improve fitness. Our results concerning the kin selection hypothesis partly contrast with those of the the first jackdaw study but not with the second one. De Kort et al (2006) found no effect of kinship on cofeeding rate, in their experimental group. In von Bayern et al (2007) study, the three main dyads still sharing food at the end of the testing period were heterosexual pairs but were also all sibling pairs. One of the crystallized sibling dyad was a trio: one female, which was paired with her brother kept sharing food with another female. Consequently, it was not possible to conclude unambiguously whether food transfers were driven by kin selection or pair-formation. The fact that the birds shared mostly with one exclusive partner from the opposite sex pointed at the pair bond formation explanation more strongly. In our cockatiel group, one of the two heterosexual mated pair was also formed by siblings.

It has been pointed out that formations of sibling pairs as well as same-sex pairs in corvids may be an artifact of captivity and some disruption of the natural process of pair-bond formation due to the limited choice of possible partners and therefore should be interpreted

with caution (de Kort et al., 2003) (von Bayern et al., 2007). The same might apply to parrots and a caveat of our study is that the sample size was small. Moreover, even if the group was constituted of five males and five females the sex-ratio was biased inside each sub-group: the group of siblings was mostly constituted of males and the group of unrelated individuals was mostly constituted of females. It is a possibility that the choice of partner was constrained by this biased sex-ratio inside each subgroup. This could have biased our results into more sibling pairs and same-sex pairs than would have formed with a greater choice.

However, in another small parrot species, Spectacled Parrotlet (*Forpus conspicillatus*), it has been observed that in the first months of life, courtship feeding and reproductive behavior of captive birds are addressed predominantly to siblings, preceding the final pair-bond formation with an unrelated bird of the opposite sex in sexually matured individuals (Garnetzke-Stollmann & Franck, 1991) (Wanker, Bernate, & Franck, 1996). Similarly, in budgerigars, fledglings form mutual affiliative relationship including cofeeding and allopreening with one of their siblings before elaborating a stable pair with an unrelated individual (Stamps, Kus, Clark, & Arrowood, 1990). This process may be a crucial developmental learning phase for the young birds to acquire social rules and an appropriate behavior with their conspecifics. Even if cofeeding between siblings in these cases can be interpreted as some courtship behavior, it seems more implicated in constructing the young bird social life rather than in real pair bond formation. These ephemeral associations with siblings could be seen as a training period before bonding with an exclusive partner. The two examples of other parrot species may suggest that, in these two species and in cockatiels, a combination of both kin selection as well as the pair-bond formation hypothesis best explain their cofeeding patterns

Our results are also in line with the reciprocity hypothesis (Trivers, 1971). The studied cockatiels transferred food mainly to those from whom they also received food. This may suggest a tit-for-tat dynamic in the food exchanges. On the other hand the affiliative

behaviours indicated that the birds that mutually shared food were also affiliated as siblings. Hence, their food-sharing was probably driven by the degree of affiliation rather than by the motivation to reciprocate. One may also argue that the reciprocal cofeeding pattern was, simply because cockatiel siblings spend most of their time in close proximity. De Kort et al (2006) observed a similar food-for-food pattern in the study on young jackdaws and argued that proximity could not be the main driving motivation to exchange food since some of the individuals shared with up to 8 partners within a single feeding trial. This finding suggested that the donor actively approached partners and fed them. The fact they all received food from the donor in the same trial could not be explained by their proximity with the donor. Similarly, in our study donors sometimes shared food with multiple individuals. Also, there was clearly no reciprocity in stealing, even if stealing attempts also occurred between birds sharing strong bonds and spatial proximity. This finding indicates that proximity was not the underlying explanation for cofeeding.

Cofeeding was also correlated with allopreening, which one may interpret as indicating an interchange between cofeeding and affiliative behaviors. Consequently our results are also in line with the trade hypothesis, suggesting that reciprocation can occur in a different currency (Noë & Hammerstein, 1995). This kind of exchange has already been observed in several primate species e.g. chimpanzees (de Waal, 1989 ; de Waal, 1997a) but also in vampire bats, in which food-sharing was positively correlated with grooming (Wilkinson, 1986). Whether the observed cofeeding patterns indeed are a calculated exchange of favors, rather than just reflecting the individuals' mutual affiliative bonds, remains questionable. Affiliative behaviours such as preening (or grooming) are also manifestations of existing affiliative bonds and may also reflect its strength. In vampire bats for example, it has been suggested that food-sharing may require social bonds developped over long periods of time and was most likely to happen between individuals sharing high levels of association (Carter &

Wilkinson, 2013). Whether food-sharing may also be underpinned by prosocial motivations and the will to improve others' welfare, as it has been proposed in primates (de Waal et al., 2008;de Waal, 2008), remains to be investigated. The additional observed exchange of stealing and allopreening could be an artefact of the interaction frequency between affiliated birds. Indeed, siblings interacted more than unrelated birds and as a consequence this may also include more aggressive interactions although they just represent a minor proportion considering the overall affiliative interactions. We can also underline that no stealing events occurred between females. Only female-male pairs and male same-sex pairs displayed such kind of aggressive interactions. This result is in line with a previous study which demonstrated that male cockatiels exhibited higher rates of aggression than females (Seibert & Crowell-Davis, 2001).

Another point that needs to be considered here before major conclusions can be drawn on a trade or reciprocity in different currencies argument is the temporal aspect. The analysis revealed a correlation between cofeeding and affiliative behaviors but we cannot conclude about the causation of these events because the temporality of the two behaviours in relation to each other is not taken into account. We therefore remain ignorant if the cockatiels were keener to share food after being preened or whether they preened birds more likely with whom they were allowed to cofeed before. In order to clarify the causation between socio positive behavior and willingness to share food, we would have had to analyze data with this notion of temporality.

The willingness to share also needs to be tested. Indeed, the harassment avoidance hypothesis could also be used to explain why birds are transferring the food they prefer and why they accept to lose the nutritional value of the food item. They could be forced to share by others. Contrary to jackdaws (von Bayern et al., 2007) which exhibited a distinct posture, no begging postures were observed in cockatiels. Potential receivers willing to eat the food, usually

followed donors on perches but did not call or moved their wings in a ritualized manner. However cockatiels were clearly not co-feeding in order to avoid beggars and aggressive threats by their partners: stealing events associated with aggression were scarce and there were very few harassment events. Usually, the donor easily avoided any harassment by walking off, turning their heard away from the beggar or flying away to another perch. The potential receivers rarely followed them and did not make repeated attempts. In jackdaws, a positive relation wad found between the amount of begging received by the donor and the amount of food shared with the beggar but the donor's costs of being exposed to begins remains unclear. And apparently no agonistic interactions preceded food exchanges suggesting that donor were not physically forced to share food with their partners (de Kort et al., 2006) . The study with rooks (Scheid et al., 2008) and the second study with jackdaws (von Bayern et al., 2007) did not investigate these hypothesis.

The finding that the cockatiels shared the preferred food type (fennel) more with their partners than the less preferred one, may indicate that they may have perceived a higher value item, as serving as a stronger signal. Cofeeding could support the "signaling" function, suggesting that costly behaviors, like food sharing could be used to test the quality of a mate (Zahavi, 1975). It was the main explanation for food-offering, but not for cofeeding in rooks, since dominant members of the dyad offered food significantly more than subordinate members. However no such significant effect of dominance was found for cofeeding (Scheid et al., 2008). The same trade was observed in jackdaws: jackdaws active giving took place from subordinates to dominants and vice versa. These findings do not support the prestige-enhancing and dominance-affirming hypotheses, which predict that active giving only takes place from dominant to subordinates (de Kort et al., 2006). This hypothesis has not been tested with cockatiels but it is unlikely that dominance played a role in cofeeding in these birds, since many individuals acted both as recipients and donors with many partners

Alternatively, the birds may use it as a more effective trading currency. In primates the quality of the item can impact on the sharing rate as shown e.g. in chimpanzees (Boesch & Boesch, 1989; Rose, 1997), humans (Kaplan et al., 1985) and capuchins (de Waal, 2000). These species have been shown to share meat more extensively than plant-food. Since meat is more difficult to obtain and a better source of energy, it represents a high quality and valuable trading item (Kaplan et al., 1985) but the taste preference has not been tested in these cases. In our study, both carrot and fennel were rare, but the nutritional value and the energy benefits for the birds have not been evaluated, even if carrot is suspected to represent a higher nutritional value, due to a higher proportion of carbohydrates. Interestingly, in previous studies on jackdaws, contrasting results have been observed: birds shared the preferred food significantly more in the first study (de Kort et al., 2006) but the jackdaws in the following study, showed the opposite trend and kept the preferred food mostly for themselves (von Bayern et al., 2007). In the first study, it has been argued that the excess of active giving of preferred food cannot be explained by the begging rates of the recipient. Cofeeding may be in this case the signal of positive intent towards the recipient (de Kort et al., 2006). Contrary to cofeeding, the motivation to steal in cockatiels was not influenced by the quality of food, suggesting that the exchange of preferred food could be, as it has been suggested by de Kort and co-workers (2006) the signal of a positive intent and a prosocial action directed towards a conspecific to improve its welfare.

Affiliation seems to play a crucial role in food sharing since siblings, which also exchange a lot of affiliative behaviors, are also the birds who shared food at the highest rate. It would be very interesting to test food-sharing during the breeding season and also during the rearing period of nestling to see if in these conditions partners would exchange more food. Interestingly, in adult jackdaws, food sharing only occurred between mated partners. In the

food-sharing experiment with cockatiels, birds were young adults, and it is likely that they were still choosing their future sexual partners. Thus, more observations when mates would have lay eggs would be useful to better understand the implication of food-sharing in bond formation.

b) Testing prosociality in an artificial task with psittacids

The aim of the third study was also to investigate prosociality in psittacids, this time via a Prosocial Choice Task (PST) using token exchanges in an artificial setting involving an interaction with a human experimenter. In the first experiment, dyads of birds had to choose a token in front of a human experimenter. The bird chose one out of three tokens. Each token was associated with a specific value: the no-reward one which gave no reward at all, the own-reward token, which provided a reward only to the subject and the both-reward which gave access to a reward for both participants. The dyads of birds were either sexual partners, or siblings, or only familiar birds housed together.

Experience 1: Other-regarding preferences in psittacids

In the first experiment, we tested eight individuals from four different species and, except for the male *A. macao*, we observed that all birds rapidly stopped to choose the "no reward" object. Moreover, Shango and Zoé emitted more frustration calls when the subject chose the "own reward" object than the "both reward" one. The same observations were made while testing two other african grey parrots on the same paradigm. Indeed, one bird emitted more frustration calls and asked for the reward ("want nut") when seeing all or part of the reward going to the partner (Péron et al., 2013).

In this experiment, African grey parrots did not choose more often the "both reward" item than the other parrots but they definitely vocalized more. Conures and macaws did not express their frustration via calls. It is possible that being tested with a sibling or a mate and seeing it

receiving a reward is less frustrating than being tested with a non-mate or a non-sibling. Indeed, even though they were housed together, African grey parrots did not display strong bonds as seen within mated pairs.

Also, the male *A. glaucogularis* has been observed once displaying aggressive behaviors towards its female after she picked the "own reward" item. These reactions indicated that the bird understood the value of each item and that he would not receive any reward due to its partner's choice. We can conclude that most of these birds can attribute a value to the objects and discriminate between them according to the outcome. We chose not to use an item which would only reward the partner because we used it in a previous experiment and the birds avoided this choice (Péron et al., 2013).

Similarly to chimpanzees (Silk et al. 2005; Vonk et al. 2008), cottontop tamarins (Cronin et al., 2009) and jackdaws (Schwab et al., 2012), our psittacids did not always deliver food to a partner at no supplementary cost although some partners were siblings or mates.

However, and contrary to our hypothesis, no links have been clearly demonstrated between affiiation and prosociality. Contrary to our expectations, African grey parrots did not change their strategies according to their partner. It is surprising to observe that Zoé, the female African grey parrot, kept choosing the "own reward" object most of the time, even at the end of the experiment, and with her two partners, even though she shared different relationships with them. We thought that she would change her strategy depending on her partner identity: choosing more "both reward" items with Léo, with whom she shared affinity and chosing more often the "own reward" item with Shango, because he was aggressive with her. Instead she kept the same strategy across the three sets. A recent study demonstrated that unrelated non-pair-bonded adult pinyon jays actively and spontaneously shared food. It appeared that dominant individuals shared more than subordinates and that reciprocity did not account for sharing (Duque & Stevens, 2016). It would be interesting to study the implication of

dominance with prosociality in parrots, but it seems that their social organisation could differ strongly from corvids social associations like ravens or azured-winged magpies (Wascher and Bugnyar 2013; Horn et al. 2016). In a previous study in which the birds had to cooperate (Péron et al., 2011b), tolerance and dominance have been assessed between the three African grey parrots and we did not observe any linear hierarchy between individuals: Léo was strongly dominant over Shango, Shango was dominant over Zoé and there were no dominance between Zoé and Léo. No dominance and tolerance tests have been conducted on macaws and conures because partners were mates or siblings and were very tolerant toward each other. More investigations on social dominance and hierarchy in psittacids would be needed before investigating their links with prosociality and cooperation.

Surprisingly, we still observed selfish behaviors (choosing preferentially the "own reward" item.) with conures and macaws, even if they were exclusively tested with their siblings or mated partners.

Apparently, birds usually stick to one strategy (with the same set of objects, at least) and did not modulate it according to their partner or to the nature of the relationship they share with them. It seems to be the case for the male *A.macao* who kept choosing the "no reward" object at an important rate. Although he did not receive any reward, the experimenter reported that this bird kept choosing the same items, several trials in a row. So it is also possible that the bird was more interested by interacting with the item and the experimenter than by the reward he could obtain. To exclude any alternative hypothesis, it would be crucial to test birds in a similar paradigm but with different partners sharing different kind of relationships (mated partner, but also non-affiliated birds) in order to characterize the link between birds and the impact it could have on prosociality.

The fact that birds generally tend to prefer the same item as their partner could be seen as a form of reciprocity. Thus when one individual develops a preference for the "own reward"

object, its partner tends to do the same even if the set of objects are different for each subject. However, during another study where two grey parrots had the opportunity to take turn after each trial, we did not observe any reciprocity (Péron et al., 2013)

Interestingly, even if partners from the same dyad seemed to adopt the same strategy, the birds were not firmly and definitively stuck in their initial preferences. We could indeed observe a switch of strategies between set 2 and set 3: birds chose the "own reward" object, the selfish alternative in set 2, while they mainly chose the "both reward" item, the prosocial option with the last set of items. Like chimpanzees (Brosnan & de Waal, 2005), the birds in set 2 did not maximise the benefits they could possibly obtain because they could have chosen the "both reward" object each time and both individuals would have received a reward in each trial.

It appears that the emergence of the prosocial choice could be due to different factors. Birds tended to develop a preference for the "both reward" object near the end of the testing period, which suggests that they could have learned the consequences of the "both reward" choice. Maybe they learned to act prosocially in order to improve their partner's welfare. The subject could possibly feel positive feelings associated with improvement of another's condition i.e., the "warm glow" effect; (Andreoni 1990; Imas 2014). During another experiment conducted with two other African grey parrots tested with human partners in another lab, one bird responded in ways that suggested he understood reciprocity and prosocial behaviour at some level (Péron et al., 2013). In cottontop tamarins, reciprocity increased food transfers. However, when tamarins' behavior was evaluated in relation to the non-social control, a prosocial effect emerged late in sessions independent of reciprocity (Cronin, Schroeder, & Snowdon, 2010). So we cannot exclude the fact that prosociality emerges across trials and could be stimulated by the fact to see partners being rewarded.

It also appears that with *A. solstitialis* and *A. glaucogulatis* birds, partners sometimes tried to steal food from the subjects when they chose the "own reward" object. Another possibility would be that prosociality could be chosen in order to avoid stealing and maximise the reward obtained by the subject. That way, both birds obtained a reward and there was less chances that the partner try to steal food from the subject. Even though we did not observe any begging behaviors or direct harassment as it has been described in primates, the partner's behaviour of stealing in the "own reward" alternative could influence the subject's preference for the "both reward item". Indeed, a harassment model predicted that the more insistent the beggars will be, the more the sharing by owners will increase (Stevens & Stephens, 2002). Such findings have been observed in several primates species as chimpanzees and squirrel monkeys (Stevens, 2004).

The male *A. glaucogularis* twice stole the reward from its female during trials in which he picked up the "both reward" object. It is possible that in this situation, in which both birds received a reward and the total amount of food was split, a negative association was formed because the birds had to 'share'. We could also hypothesize that subjects chose the "both reward" item in order to steal it from the partner and obtain two rewards instead of one. Nevertheless, these stealing attempts were too rare to represent the main motivation to act prosocially.

Even if some rare events of stealing and aggression have been recorded, no changes in social interactions (e.g., no affiliative behaviours or attacks) were displayed just after the testing period (behaviours have been recorded during fifteen minutes following the end of the session) but maybe longer observational periods post session would have revealed some differences.

Finally, the fact that birds chose preferentially the "both reward" option at the end of the experience could be due to pure chance. Indeed, as we observed an important switch in

strategies between set 2 and set 3, results could be different after another replication. Birds clearly made a difference between the items delivering a reward with the "no reward" items, but it seems they alternated their choices between the prosocial and the selfish options. Similarly, it has been shown in another study that captive blue jays tested in controlled-payoff games do not cooperate in the absence of immediate benefit, even if a long-term benefit may exist. Birds favoured short-term consequences (Stevens, 2004). In our study, birds indeed chose a rewarding item, but show no stable preferences for the "both reward" item. As long as the item provided a reward to the subject, it could be preferred.

To conclude, we must stay careful with the interpretation of these data. As intra- and inter-individual differences are significant, more individuals should be tested with more different sets of objects to reach a definitive conclusion.

It seems that prosociality emerges across sessions, but more replications would be needed to acertain it.

Experience 2: Influence of inequity onother-regarding preferences

When the value of the "both reward" item was modified to create inequity, birds seemed to stick to their previous preferences in both control and inequity conditions when we studied their individual strategies: the two males chose preferentially the "both reward" item while Zoé, the female, kept choosing the "own reward" object. The birds did not react similarly to capuchins monkeys who stopped being prosocial when the differences between the outcome for the tested individuals and the one for its partner were too high (Brosnan, Talbot, Ahlgren, Lambeth, & Schapiro, 2010). Like chimpanzees (Bräuer et al. 2006), our African grey parrots did not behave much differently when faced with an unfair situation. The males continued to prefer the "both reward" item, perhaps because they did not care about the reward value (they

did not either stop working, as capuchins or chimpanzees sometimes did in such an unfair situation).

Even though birds have been tested alternatively in control condition with a food they were used to, and in inequity condition with a preferred food given as a reward to the partner, subjects did not really show frustration. Since, in inequity condition, both birds received food at the same time, it appeared that the frustration was not strong enough to create IA.

We can also argue that the subject did not pay attention to the partner and the reward he received, as the subject had its own reward to eat at the same moment. Indeed, both birds were rewarded at the same time, and since the partner was perched 50 cm away from the subject, it is possible that the partner and its rewards were not cues of interest for the subject at this very precise time.

Possibly their inequity aversion (IA), if present at all, was not strong enough (as they still received a reward) to overrule a previously established preference. The high number of trials they received during the first experiment, could also play a role in this fixed, previously learned strategy.

Moreover, as previously stated, it has been shown in primates species that effort could play a major role in IA (Massen et al., 2012). In our task the partner received food while being totally passive (the partner bird was perched next to the subject and just had to wait to obtain a reward) and the subject only had to choose an item. The results obtained with African grey parrots are close to those obtained in orangutans and squirrel monkeys when tested in a token exchange paradigm with an experimenter (Brosnan et al. 2011; Talbot et al. 2011). In chimpanzees, it has been also described that individuals did not respond to inequity of rewards when those rewards were simply handed to the individuals without a task being required (Brosnan et al., 2010). Consequently, it would be interesting to increase the level of

inequity between rewards to observe if it has consequences on the birds' willingness to participate to the task.

Besides, as stated by Silberberg et al. (2009), IA is supposed to emerge if the subject is exposed to having the quality of its reward degraded across the condition. In our study, it is not the case: in inequity condition, when the subject chose the "both reward" option, he received the same "usual" food as before, and the partner received a better reward. In this experiment, the subject's rewards have never been directly impacted. It would be interesting to test parrots with a degradation of the food reward across time in order to test if IA would emerge in this setting.

In spite of all, we observed a surprising result within interactions: there was a significant difference between inequity and control conditions within the "both reward" item' choice. It was probably due to Zoe's choices, which were more random than the males' choices and introduced this variability in our results. This result is contrasting with all studies about IA, since most animals kept choosing the same strategy than before, or stopped to cooperate when the partner received a better reward. In birds, crows and ravens have been tested in a token exchange task to evaluate their behavioural responses to inequity in the quality of reward (Wascher & Bugnyar, 2013). Contrary to our parrots, corvids decreased their exchanges when the experimental partner received the reward as a gift, for "free" (without exchanging a token first). They also decreased their exchange performance in the inequity condition compared to the equity condition, and even refused to take the reward after a successful exchange in inequity condition compared to other conditions. Once again, it seems that IA was linked in this paradigm with the working effort necessary to obtain the reward.

However, animals do not always respond to inequity, and even when some animals respond to IA, some individuals do not (Bräuer et al. 2006; Bräuer et al. 2009; (Brosnan, Schiff, & de

Waal, 2005). It is still crucial to underline that very few studies have been conducted in birds and more investigations are needed to identify the factors that moderate the response to inequity aversion.

Experiment 3: Influence of other-regarding preferences on the maintenance of cooperative behavior

In this third experiment, birds had to cooperate to obtain a reward. The subject (Léo) had to choose one token, then gave it to the receiver, which had to put it in the experimenter's hand to be rewarded. In this experiment the subject still avoided the no-reward token but did not choose preferentially the both reward token over the own-reward one. Interestingly the receiver (Shango) cooperated less when he received the own-reward token, which provided him no reward. Sometimes, the receiver even preferred to throw the "own reward" item away, than to transfer it to the experimenter. He also emitted more frustration calls and left the apparatus more often when the subject gave him the "own reward" item. Once again, we could conclude that the receiver clearly understood the value of each item, but it seemed that the subject did not take the receiver' welfare into account. Unfortunately, we could not exchange the roles of each bird and check if the previously frustrated receiver would change its strategy when becoming the subject.

The fact that Léo did not take into account the situation of its partner and did not adapt his choices to its partner's reactions could be linked to the fact that our birds did not show any differences between the two rewarding items in some of the previous trials (experiment 1). Previous studies conducted with the same birds revealed that they were able to cooperate and even to share when the reward was not equitably distributed (Péron et al., 2011b).

Even though this experiment was designed to enhance prosociality and cooperation in our birds, Leo's behaviour can be explained by simple associative learning (choosing one of the

two items that usually provided him a reward). Shango's behaviour, although more complex, could also be explained by such kind of learning (transferring only the reward which provided him a reward). As shown since a long time ago (see for example Boakes & Gaertner, 1977), even more complex cooperation tasks involving communicating some information to a partner could be interpreted in terms of associative learning and autoshaping. Maybe alternating birds' roles during the experiment could have led to different strategies (and incitate Léo to act other-regarding) and results such as reciprocal altruism (Trivers, 1971) but even in this case an interpretation in terms of associative learning could not be ruled out. Shango's aggressive behaviors toward Léo when he failed to cooperate are probably the best argument against such a parsimonious interpretation even though they were not frequent enough to be significant.

Similarly to chimpanzees (Silk et al., 2005; Vonk et al., 2008), cottontop tamarins *Saguinus oedipus* (Cronin et al., 2009) and jackdaws (Schwab et al., 2012), our psittacids did not always deliver food to a partner at no supplementary cost although some partners were siblings or mates. We could argue that the presence of food rewards could have inhibited the prosocial tendency of the subject, which was entirely focused and concentrated to obtain food for itself. Some studies suggested that when food was visible, the subject was influenced by the desire to eat the reward (Warneken et al., 2007; Barnes et al., 2008). In our experiment, the bowl filled with the rewards was on the experimenter's knees and was hidden when the subject had to choose the item, but the food was then made visible when participants ate their reward. It is then likely that the motivation for food had incidence on the subject's choices.

To conclude, most of the individuals of the different psittacids species tested in this study were able to understand the task and attribute values to objects. They chose the prosocial option at the end of the first experiment, but did not react to inequity in the second experiment

and the subject did not take its partner's reaction into account to maintain cooperation efficiently in the last experiment. However, the understanding of the task and the alue of the token seems to be validated and are encouraging results to duplicate this study with more subjects. It would be especially interesting to test individuals with different partners, depending on their degree of affiliation, as tested with African grey parrots.

2) <u>Does empathy exists in cockatiels?</u>

The aim of the second study of this thesis was to investigate the roots of empathy via behavioral responses of cockatiels to distress calls of familiar birds. We wanted to determine if the intensity of their behavioral responses was modulated by affiliation and by the potential emotional bonds existing between partners. Four variables were used to quantify the stress-induced responses of these birds (locomotion, the number of calls emitted, the time spend near the loudspeaker and the time spend with their crest of feathers erected).

Our results demonstrate that during the playback stimuli, the cockatiels reacted more intensely (as expressed by the number of calls, the activity of the bird, or the time spent near the loudspeaker) to distress calls of conspecifics than to control noise. The birds responded more strongly to partner distress calls than to non-partner distress calls in terms of all recorded stress-related behaviours (activity levels, avoidance of the loudspeaker and crest position) during the playback, except for the number of calls.

Also after playback stimulation, the cockatiels appeared to react less to white noise than to conspecific distress calls, although they appeared generally more aroused after a playback of either condition than before, as one would expect. This reconciles with the findings of a previous study which demonstrated that white noise elicited changes in behavior over no noise in budgerigars *Melopsittacus undulatus* (Miller et al., 2012a). Our cockatiels reacted differently to conspecific calls and white noise but they also displayed an increased attentional state during white noise stimulations similarly to budgerigars, often showing crest position 1

(i.e., crest fully erected). Moreover, no significant differences were found in crest position during playbacks of non-partner distress calls versus white noise. This result suggests that the birds were attentive in both conditions. More intense reactions to conspecific calls compared to control noise have also been reported from domestic dogs (*Canis familiaris*) which exhibited more stress-related behaviours when exposed to conspecifics' whines than when hearing control stimuli (Quervel-Chaumette et al., 2016).

Our finding aligns with other reports of animals that discriminating between conspecific calls depending on the degree of affiliation. Similar results were observed with adult ravens (*Corvus corax*) which heard playback calls from previously familiar ravens with whom they shared an affiliate or non-affiliate relationship and from unfamiliar ravens whom the birds had not encountered before. Ravens separated for up to three years responded differently to playbacks in call numbers and call modulation depending on the valence of their relationships with the emitter of the calls (Boeckle & Bugnyar, 2012). However, these studies did not investigate emotional responses specifically. More interestingly, a study investigating emotional contagion, but not discrimination between conspecific calls, revealed that the contagiousness of yawning in females geladas baboons correlated with affiliation and the level of grooming contact between partners (Palagi et al., 2009). Since studies investigating the discrimination of calls based on affiliation are rare, we also looked at results involving familiar animals. Domestic horses (*Equus caballus*) can discriminate conspecifics depending on familiarity: they exhibited significant changes in head orientation depending on the category of whinnies they had been exposed to. The strongest orientation was displayed in response to unfamiliar calls, the lowest in response to group member calls and intermediate responses to familiar calls (Lemasson et al., 2009).. A study examining emotional responses on domestic dogs compared reactions to familiar and unfamiliar conspecifics vocalisations

using a paradigm similar to ours, but failed to find any significant difference (Quervel-Chaumette et al., 2016).

In our study, intense behavioural responses indicating emotional arousal/mild stress were only observed during the playback stimulations. It is important to emphasize that hardly any such stress-induced behaviours were observed before the first playback stimulation, suggesting that social isolation in itself or the handling at the beginning of the experiment were not sufficient to elicit any observable arousal. Before the first playback stimulus, the birds were not very active. They typically sat calmly on the floor and appeared sleepy at the end of the "before" phase preceding the playback. This sleepiness could have been a consequence of the stress they felt before the beginning of the experiment, as it has been observed that yawns in budgerigars were strongly elicited after a stressful handling procedure (Miller et al., 2010). Nevertheless, before the playback, the birds did not emit any calls, they spent more time near the loudspeaker (the source of a stressor in the experiment) than during and after the playback and had their crests down, which suggest that birds were calm and relaxed. In other social bird species like zebra finches (*Taeniopygia guttata*) social isolation in itself can impact on the birds' behaviour and physiology. In zebra finches social isolation results in a lower vocal activity and a rise in plasma corticosterone (Perez et al., 2012). Consequently, we kept the experimental phase as short as possible (30 minutes maximum) and used a 10-minutes period of silence at the beginning of the experiment to allow birds to calm down before the playback stimulation in order to reduce any potential bias due to the stress of the preceding procedure.

Movement is a common variable used to quantify behavioural responses to distress calls. However conflicting results have been reported in different species. Some species move less and freeze more often when they perceive a conspecific's distress (Gonzalez-Liencres et al., 2014; Goumon & Špinka, 2016), while other species' movement patterns seem unaffected or actually increase in response to conspecific distress calls. A study on pigs for example found

no differences in their movement patterns depending on whether the pigs heard sounds of conspecific in distress or control sounds (Düpjan et al., 2011). Indian mynahs *(Acridotheres tristis)* increased their flight and walking rates when exposed to a taxidermic model hawk associated to conspecific distress calls, as compared to blank controls trials (Griffin, 2008). Thus, in some bird species, an increase of locomotor activity when exposed to distress calls seems to reflect stress-induced behaviour and the motivation of the bird to escape. It is interesting to underline that during playback of white noise, the cockatiels did not move but seemed highly attentive (they stared without blinking, did not move and displayed an erected crest), possibly to gain information about this novel stimulus.

Alarm call production in cockatiels compares with that of other species that produce alarm calls in fearful situations: their calls have short durations, they are tonal with high frequencies and exhibit frequency modulations (Briefer, 2012). In our present study, it is worth emphasizing that no bird called before the playback stimulation, and only 4 individuals emitted the 9 calls produced overall during the silent phases following the broadcast, which may suggest that the alarm calls are directly triggered during the playback stimulation and are a manifestation of the emotional arousal of the subject. The birds mainly produced calls during the playback stimulus and significantly more in response to conspecifc distress calls compared to white noise. However, there were no differences in the number of calls emitted by the subject when hearing partner or non-partners distress calls. Conspecific calls are probably very strong stimuli when testing social birds in isolation. This salience may have caused a ceiling effect so that no differences could be found between the two types of conspecific calls in terms of calls emitted in response.

In some species the type of alarms calls have been found to vary in relation to the size or type of the predator and/or the urgency of the response (Evans et al., 1993; Blumstein, 1995; Manser, 2001). For instance, black-capped chickadees (*Poecile atricapillus)* increased their

calling rates in the presence of smaller predators, expressing a higher risk, than when encountering larger predators or controls (Templeton et al., 2005). In our present study, one might hypothesize that birds would call more when a close partner is in danger than when a non-partner is in a similar situation. Thus, the number of alarm calls emitted would translate the emergency of the response through the emotional state of the emitter and the signal would be both referential and emotional (Seyfarth & Cheney, 2003a, 2003b). Given that only few birds emitted calls during the playback stimulus (6 out of 10 birds called and emitted 97 calls in total throughout all playback phases) and that important individual variations exist between subjects, our sample size was too small to show any significant differences.

Some distress calls are known to elicit strong aversive reactions and immediate flight responses in different species. Such calls have been even used in airports to scare away birds from aircrafts (Papin, Sebe, & Aubin, 2015). However some bird and bat species' distress calls both alert conspecifics but may also trigger their mobbing behaviour, thus attracting conspecifics (Fenton et al., 1976; Russ et al., 1998; Branch & Freeberg, 2012). In the case of our study, it was not possible to make final conclusions about the function of distress calls in cockatiels, given that their movements were restrained by the cage, so that they could not show flight or mobbing responses. Yet, the playback of distress calls in our study seems to have triggered stress-induced behaviours that would normally result in flight more than any sort of mobbing behaviour. The subjects significantly avoided the loudspeaker during the playback (but not before or after the playback stimulus) suggestive of an aversive reaction to the distress calls playbacks.

Motivated by an ever growing concern of improving animal welfare, the last 10 years have brought about many studies investigating how to interpret and measure emotional processes in animals (Paul et al., 2005, Mendl et al., 2010; Briefer et al., 2015b). There is a general consensus that emotion can be measured via behavioural, cognitive and physiological

changes. Physiological measures such as heart rates (Wascher et al., 2008a, 2008b; Briefer et al., 2015a; Düpjan et al., 2011; Goumon & Špinka, 2016) or hormonal levels like salivary cortisol (Perez et al., 2015; Mariappan et al., 2013) have been used to assess emotional responses in different species. However, they did not always find significant differences between control and aversive conditions, and often the data did not seem reliable since it is often difficult to control for excitement caused by the test procedure (Quervel-Chaumette et al., 2016; Düpjan et al., 2011; Goumon & Špinka, 2016; Reimert et al., 2013). Given these difficulties, we chose to focus our investigations on non-invasive behavioural measures, which were easy to apply to our small avian model.

Most of the studies on emotional processes have been conducted on mammals and it was our goal to develop new tools to measure behavioural responses in birds in this particular context. The use of the crest position, even if it can indicate either attentional state or stress-induced reactions, proved to be a relevant indicator in this species. Cockatiels generally use their plumage to express emotional states and they displayed erected crests more during the playback stimuli than before and responded more strongly to a partner distress call than to a non-partner's distress. Birds are known to puff their feathers to express emotional arousal in several contexts such as during agonistic interactions. It is for example the case in jackdaws with the "bill-down" posture which is a threat posture characterized by an erect body position combined with fluffed head and body feathers (Lockie, 1956; Röell, 1978). The position of facial and head feathers could be used in other species of birds to assess emotional states. Our results are promising and encourage further development of this measure.

To summarize, cockatiels reacted more strongly to conspecific distress calls compared to a control sound, but interestingly they reacted differently depending on the identity of the emitter and the degree of affiliation between them. Although we did not measure the emotional valence of the played back distress calls and the alarm calls recorded in response to

the playbacks, and although we only focused on negatively valued calls, our results suggest that it may be promising to assess emotional contagion in psittacids further. We observed that movement patterns, vocalizations and distance to the loudspeaker were informative and yielded differential results depending on the degree of affiliation between the subject and the caller. We also found that recording the crest feather position constituted a meaningful new indicator of attentiveness and emotional arousal in cockatiels. Looking at feather positions may provide a new, non-invasive technique to measure stress response and attentional state in birds and deserves more attention by further studies.

Our results are especially striking because birds not only reacted to these distress call stimuli, but they distinguished the identity of the caller and they responded differently depending on the identity of the emitter and the relation they shared with the subject. These results were not observed in similar paradigms with dogs (Quervel-Chaumette et al., 2016).

Our results reveal that birds reacted differently depending on the relationships they shared with emitters, suggesting that the preferential bond they share drove the intensity of their behavioral reactions. Nevertheless it would have been interesting to test more types of dyads in order to understand if one kind of relationship (like the one shared by mates) would trigger more intense reactions than others. Is it the duration of the association (siblings know each other since they were born) or its functionality (reproductive success of mates) that could influence the emotional link between partners? Due to our small sample size, we could not compare the intensity of reactions depending on the type of dyads (mates, siblings or affiliates). Even if our results are not sufficient to prove the existence of empathy-mediated responses in cockatiels, these differential responses to audio stimuli are first evidences of preferential sensitivities towards others.

Empathy could have evolved in animals in order to form and maintain bonds within social groups and to help others while responding to their needs (de Waal, 2008). One of the most

popular hypotheses explaining the origin of empathy is parental care. Taking care of offspring increases fitness but is also mediated by attachment (Decety et al., 2016). It has been argued that empathy could motivate parental care and would have been selected because it increases fitness by maximizing the survival of offsprings. In birds, most species form monogamous pair bonds and biparental care is common. Some birds even form long-term pair-bonds like jackdaws (Kubitza et al., 2015) or pair-bonds for life like barnacle geese (Black, 2001). It has even been observed that the efficient cooperation of parents at the nest is required for the survival of the offspring, unaided females having more difficulties or even failing to take care of broods by themselves (Wolf et al., 1988; Dunn & Hannon, 1989). It could then be argued that long-term monogamy and biparental care in birds could be especially convenient to study the role and influence of empathy. More studies are thus required to investigate these questions.

3) Impact of pair-bonding on behavioral responses in a stressful situation

The aim of the last and fourth study was to evaluate the impact of the social relationships on novel object exploration in neophobic jackdaws. Birds were exposed to 6 different situations: a control, in which preferred food was presented in a bowl and random exposure to novel objects of 5 different categories which were presented next to the food and which differed in intimidation level. They were exposed to these stimuli either alone, with their mate or with a familiar opposite-sex partner. The study shows three main results. First, the jackdaws exhibited certain preferences for their mate (i.e. the partner). Mated pairs were seen in proximity to each other more often, when in an intimidating than when in a non-intimidating situation, whereas the opposite was true for non-partners. Moreover, more aggressive displays occurred between non-partners than between partners. Second, the explorative behavior of the jackdaws appeared affected by the condition yet two different patterns were recognizable that

depended on the individuals' tendency to explore (i.e. all individuals were ranked accordingly). The less explorative birds were quicker to approach the object when tested with their mate than when tested alone or with another bird whereas the more explorative birds always approached very quickly independently of the social context. The more explorative birds also were more likely to touch objects when alone compared to social contexts, while the less explorative birds surprisingly were most likely to touch an object when paired with a non-partner. Third, there was a general effect of sex with females being slower and less explorative than males, when all conditions were jointly considered. Also, females were slower to start eating when tested alone than when with another bird, particularly with their mate, whereas no such differences were observed in males

The fact that mates spent more time in proximity in intimidating situations than in non-intimidating ones, while the opposite pattern was observed when non-partners were paired up suggests that, to some extent, birds actively seek reassurance in the presence of their bonding partner in stressful situations, whereas the proximity of a non-affiliated individual may not be reassuring. The result that the jackdaws stay near their mate in intimidating contexts, is in accordance with several historic studies that showed that rats sought the proximity of conspecifics in a stressful situation (Taylor, 1981) and that the presence of a conspecific reduced the fear response (Davitz & Mason, 1955; Latané et al., 1972). Rats exhibited shorter freezing periods in response to a stressful noise when placed in groups than when tested alone (Taylor, 1981). For example, rats spent most of their time in close proximity when tested with their partner and stayed much closer together than expected by chance. Gregariousness and fear reduction increased over the length of the experiment (Latané, 1969). More recent studies in other animals showed e.g. that heifers are less stressed and tried to escape less from an unfamiliar place when paired with familiar individuals rather than with unfamiliar individuals (Takeda et al., 2003). Being in close proximity in an intimidating situation therefore may have

a comparable appeasing and stress-reducing effect in jackdaws as observed during consolation in ravens (Fraser & Bugnyar, 2010a), chimpanzees (Palagi et al., 2006; Romero & de Waal, 2010) and canids (Palagi & Cordoni, 2009; Cools, Van Hout, & Nelissen, 2008).

The observation that the partners however do not seem to stick together in non-intimidating situations whereas they then suddenly stay close to non-partners asks for an explanation. One may have predicted that the birds prefer to spend time in proximity of their mate rather than another bird in any situation, as it is observed in ravens which spend generally more time in proximity with their preferred partners (siblings) (Stöwe et al., 2006a). One possibility is that the proximity with the non-partner may be an effect of social facilitation. Social facilitation means that the behavior of one individual affects the behavior of another (Zajonc, 1965). In the present study, jackdaws would spend time in proximity with other conspecifics because the context of the experience may attract birds together, even if they are not mates. The presence of a conspecific is generally positive and bring informations to the subject. Previous studies have found that jackdaws responded more to non-affiliated individuals than to affiliated individuals in a social learning context where they were allowed to watch either affiliated or non-affiliated individuals interacting with objects (Schwab et al., 2008a).

Another possibility is that non-partners stayed close together because of an arising food-competition; particularly in non-intimidating situations. Indeed, our experimental design included the possibility to obtain rare preferred food. It may be possible that the competition for food caused delay in exploration when birds are tested with a non-partner companion. While in many corvids, partners typically do not compete for food but are generally tolerant of each other during feeding and even actively share food (de Kort et al., 2006 ; von Bayern et al., 2007; Duque & Stevens, 2016), non-partners may be perceived as competitors with whom one should compete for the available food in the bowl and therefore stay close not to allow the other an advantage while feeding. When tested alone, the subject faces no danger of receiving

aggression from a potential competitor, nor when paired with their mate given that jackdaws are extremely tolerant of their partner so they are expected to come quickly eat. Even if a strong hierarchy and competition for resources (in particular for nest sites) may exist between individuals in jackdaws, (Röell & Bossema, 1982), mated pairs typically exhibit the same dominance rank within the group (Lorenz, 1931). If food competition was high between mated partners, we should have found more aggressive behaviors between mates but we found the opposite. Females also approached later when they were tested alone, suggesting that the delay to approach was not influenced by food competition with a partner but rather by their confidence to explore new objects, which appeared increased when with a partner in the case of females.

However, to our knowledge, the present study is the first to investigate the role of the social facilitation by long-term bonding partners on exploratory behavior in birds. Few studies investigated the relation between mated individuals in birds outside the reproductive context and the potential connectedness between mates. Even though mated birds are well known to form strong long-term monogamous pair bonds (Lack, 1940; Emery et al., 2007) and can be characterized by the large amount of time they spend in close proximity (Trillmich, 1976a; Boucherie et al., 2016), no experimental studies assessed how the presence of the mate could influence the subject's behavior.

Previous studies investigating exploratory behavior and the impact of the social context have compared situations where the subject was alone, with another bird (usually a sibling) or in a group with familiar conspecifics (Stöwe et al., 2006a; Moretti et al., 2015; Miller et al., 2015), but they did not compare dyadic situations in which the subject was either with a mate or with a non-affiliated familiar individual as in our study. Nevertheless, these previous studies suggested that the relationship shared by individuals influenced their explorative behavior. For example, in dogs and wolves (Moretti et al., 2015), sibling pairs investigated the object

for longer than non-siblings pairs and in ravens, siblings approached faster than non-siblings (Stöwe et al., 2006a). Juveniles ravens also handled significantly longer the target object that a sibling handled previously in the demonstrator phase (Schwab et al., 2008b).

In our study the more explorative birds always explored the objects very fast in all conditions and were more likely to touch the object when tested alone than when tested with another bird irrespective of the relationship between them. Similar results were observed in ravens in which individuals exhibited a shorter latency to explore new objects when on their own than when in a dyadic situation (Stöwe et al., 2006a). The alone condition may best represents the individual's explorative tendency without being influenced by many other potential variables. Moreover, fast ravens were also quicker to approach novel objects when alone than when paired with another bird (Stöwe & Kotrschal, 2007). One may also argue that single birds might have been faster to approach novel objects because they did not spend time interacting with conspecifics, as when tested with companions (Mainwaring et al., 2011). Generally, the delay observed in exploration when tested with conspecifics can be explained by the fact that the subject have to process more concurrent information when tested with other individuals and need more time to analyze the situation.

The less explorative individuals on the contrary, were faster to approach when accompanied by their mate than in the other two conditions while being with their mate did not increase the number of times they touched the object. One could argue that the presence of the mate has an impact on its partner behavior and that this influence is even stronger on less explorative animals. The presence of the mate would play the role of a social facilitator. The presence of the mate would induce synchrony in partner's exploratory response, as observed in Gouldian finches *Erythrura gouldiae* (King et al., 2015). It would be interesting to characterize individual profile for each bird and observe if a "slow" bird paired with a "fast" bird would be more explorative to the effect of its partner's tendency to explore. In ravens, slow birds

approached the novel objects quicker and spent more time close to them when paired with fast siblings than when alone (Stöwe & Kotrschal, 2007).

One important confounding variable to be considered here in the two social conditions (partner /non-partner) may be the explorative rank of the other conspecific the subject is paired with in the test dyad. The presence of another conspecific may not necessarily have a calming effect (as discussed earlier), but may equally transmit tension and thus lead to an increase of fear via emotional contagion when birds are tested with other individuals (de Waal, 2008). In other words, if one individual is stressed by the novel object, it is very likely that its nervous behavior will influence the other bird negatively towards the novel situation rather than appeasing it. And this transmission may be more pronounced between partners than between non-partners, explaining the differences seen between the two social contexts in the less explorative birds when exposed to an intimidating situation. In that sense, the less explorative jackdaws may be less stressed when without a partner, i.e. in the alone condition, rather than when tested with a stressed partner.

Female jackdaws were generally less explorative than males. They were slower to approach and to eat food and were less likely to remove the object than males. A similar result was found in ravens with males being the first to approach novel objects within male-female dyads. Also, when paired with another bird, male ravens followed their conspecifics significantly more often to approach novel objects and they manipulated the objects significantly longer than females, suggesting that males may be keener to take risks. It has been argued that males may be showing off when they are in the company of females (Stöwe, et al., 2006a). Differences in explorative behavior within a pair may arise from a functional role of each partner, especially during breeding season. Even if jackdaws display biparental care (Röell, 1978), they display division of labour as part of their reproductive behavior. Only females incubate the eggs and hatchlings throughout their first week while the males

provision them with food throughout this time (Wechsler, 1989). Males may therefore have been sexually selected for being more exploratory in order to increase their foraging efficiency. In line with this, studies on zebra finches revealed that the females choose their mates depending on their exploratory behavior. Females with intermediate and high exploratory tendencies preferred exploratory males over non-exploratory ones (Schuett, et al., 2011).

To conclude, the social context in which individuals encounter a novel object, influences the explorative behavior and degree of their neophobic response in jackdaws but this effect depends on their general tendency to explore. The results reveal that the affiliative bond between birds may modulate/lessen their neophobic response and facilitate/promote exploration of novel objects, especially in less exploratory and shy birds. This suggests that not the mere presence of familiar conspecifics, but the proximity of individuals to which the subjects maintain an affiliative and thus emotional bond may have a strong calming impact in stressful situations.

According to our results, it is likely that the combination of stress and affiliation would bring mates together since they are spending much time closer in a stressful condition. This study is one of the first to investigate the emotional aspect linked to neophobia, and to our knowledge, animals were only tested alone or in social context to assess their tendency to explore. The preferential link between mates, especially between strong bonded birds like feathered apes is very likely to provide answers on their emotional connectedness and the way they represent their partner.

4) Limits of this thesis

One of the main limiting factors of this thesis is the lack of informations on social organization of wild birds. Even if they have been studied for 30 years, studies on psittacids'

socio-ecology are still scarce at the moment, especially on wild animals (see Cussen, 2017 for review). Experimental studies have been mainly conducted in artificial conditions on captive birds with low samples, usually only on a few individuals like Alex and Griffin, the African grey parrots (*Psittacus erithacus*) used in Irene Pepperberg's studies. Her team surely increased the interest for psittacids and her findings provided the first highlights on grey parrots' intelligence. They successfully investigated many various subjects like vocal communication and label acquisition (Pepperberg, 1981, 2002; Pepperberg, 2009 for review) but also self-recognition (Pepperberg et al., 1995) and object-permanence (Pepperberg & Funk, 1990; Pepperberg et al., 1997). During few years, researchers of different teams also focused on grey parrots abilities investigating many questions like vocal communication (Giret et al., 2009b, 2010, 2011), numerosity (Al Aïn, et al., 2009), the ability to wait for a delayed gratification (Vick et al., 2010; Koepke et al., 2015), inferential reasoning (Mikolasch et al., 2011; Schloegl et al., 2012) or cooperation (Péron et al., 2011b, 2013, 2014) and the understanding of human intentional actions and cues (Giret et al., 2009a; Péron et al., 2010, Péron et al., 2011a). More recently, the creation of new colonies of captive keas *Nestor notabilis* (Huber & Gajdon, 2006) and Goffin cockatoos *Cacatua goffiniana* (Auersperg et al., 2012) in Vienna permitted to increase the sample size of subjects used in experiments but also to focus on new models of avian intelligence and promote productive scientific collaborations. New questions were also investigated like tool use (Auersperg et al., 2012), social information (Huber et al., 2001), positive emotional contagion (Schwing et al., 2017) cooperation (Schwing et al., 2016) and could permit some pioneer comparative studies with corvids abilities on complex problem solving (Auersperg et al., 2011, 2015) or social play (O'Hara & Auersperg, 2017).

Despite all these recent and fascinating findings, the knowledge about socioecology of psittacids remains vague. They have not been studied for years partly because of their high

mobility and their habitat, canopy for most of the species, which is difficult to access. Our existing knowledge of parrot social structure comes from observations of social behaviors in captivity in non-natural settings, mainly on budgerigars *Melopsittacus undulatus*, which are popular pet birds since the end of the 18th century Masure & Allee, 1934; Brockway, 1964 ; Trillmich, 1976a; Trillmich, 1976b). In the wild, main studies focused on the protection of endangered species, monitoring the reproductive success of birds (Berkunsky et al., 2014; Fox & Millam, 2014) or observing individually marked birds (Eberhard, 1998). Recent studies on monk parakeets *Myiopsitta monachus* described some general association patterns commonly observed in psttacids (Juniper & Parr, 1998), highlighting the importance of pairs as the fundamental unit of parrot social structure and gave some valuable informations on fission-fusion and dominance dynamics (Hobson et al., 2014). Interestingly, some results on captive spectacled parrotlets *Forpus conspicillatus* (Wanker, 1999) and budgerigars (Stamps et al., 1990) described that siblings form very strong bonds early in their life, sometimes associated with mating behaviors and later, form true pair-bonds usually with other opposite sex partners when they become matured. This transition to siblings bond to pair-bond is especially interesting and much more observations are needed to draw a general conclusion about this type of behavior in different psittacids species. More generally, more different species of psittacids need to be tested, and observations from the wild are especially needed to better understand bonds formation between individuals.

One of the other limiting factors of this study is the small set of tools actually defined to objectively quantify emotions and more particularly positive emotions in animals based on behavioral measures. The expression of emotion in human and non-human animals has been already studied by Charles Darwin in his book "*The expression of the emotions in man and animals*" published for the first time in 1873, so the concept is not new (Darwin, 1965). However, measuring emotions involves many technical and ethical constraints when taking

physiological measure like heart rate, hormones level or body temperature. These measures have to be easy to execute andbe non-invasive in order to prevent any bias or stress increase due to the manipulation of the animals. With the emergence of concerns about animal welfare in farm animals, some studies tried to define how to quantify positive emotions (see Boissy et al., 2007 for review), empathic responses (Edgar et al., 2012) and welfare (Désiré et al., 2002) in these particular settings like for example in pigs (Wemelsfelder et al., 2000; Mendl et al., 2010), dairy cows (Fregonesi & Leaver, 2001; Sandem et al., 2006), goats (Briefer et al., 2015b), horses (Leiner & Fendt, 2011) and chickens (Nicol et al., 2011). More recently, the assessing of emotional states was expanded to other domestic animals like dogs (Kuhne et al., 2014; Rehn et al., 2014; Zupan et al.,2016). One of the aim of this thesis was also to investigate emotions in birds and to define ways to assess these emotional states without using body temperature measure (Ikkatai & Watanabe, 2015), hormones levels (Palme, et al., 2005) or heart rates (Wascher et al., 2008a, 2008b), which require costly instruments and could influence behavioral responses of subjects. Consequently, we quantified the way birds are puffing their feathers to reflect their emotional states. This behavior has been already observed in some descriptive studies, especially during agonistic interactions, and it is commonly admitted that feathers position can reflect emotion arousal in birds (Lockie, 1956; Röell, 1978; von Bayern, 2008) but no method had been clearly defined to experimentally test it. Crest positions revealed significant results in cockatiels (study 2), the birds erecting their crest differently depending on the stimulus they heard. Nevertheless, it is still difficult to distinguish attentional state from stress via feathers movement in cockatiels since no significant differences were observed between the reaction to white noise and non-partner distress calls. A more precise analysis of crest and feathers movements of cockatiels in different contexts (in group and in isolation, during both agonistic and positive interactions) should be tested.

5) Direction for future studies

1) Comparative studies between corvids and psittacids

Even if "feathered apes" are more studied at the present time than 20 years in the past, many questions about the emergence of their remarkable intelligence remain unanswered. In order to better understand how intelligence evolved in psittacids and corvids, more comparative studies are required. Indeed, these two families of bird possess all supposed pre-requisites for intelligence, as observed in primates: they have a large relative forebrain size, live in complex social groups and have a long developmental period before becoming adults (Emery, 2006). Despite these similarities and their now well demonstrated cognitive capacities, very few studies compared birds of these two families on experimental tasks (Auersperg et al., 2011, 2015; O'Hara et al., 2017). Of course, corvids and psittacids are distantly related species, they are not living in the same habitats, and have their own specificities concerning diet and social life, but comparing their performances in similar tasks would definitely bring us some valuable insights on the convergent evolution of their cognitive abilities.

I wanted to use the exact same paradigm to compare prosocial abilities in both jackdaws and cockatiels to examine similarities and differences between these two species. Jackdaws were not able to preferentially open the baited box over the empty one, contrary to what have been previously found on a very similar experiment, with other jackdaws (Schwab et al., 2012). On the other hand, cockatiels were very shy with the experimental cage and could not be tested properly. Birds clearly needed more time of habituation but it was stressful and much more complicated than for jackdaws to train the birds to go in the apparatus. Jackdaws could fly directly to the experimental room, since the access to the experimental room was always made possible and was contingent to their main aviary. Cockatiels on the contrary were housed in a lab where their housing aviary was separated from the experimental room by a long corridor.

Consequently, birds were moved in a cage from one room to another, which was stressful even if we spent time habituating them.

It would be particularly interesting to design a task which could test the prosocial abilities of both parrots and corvids with the same paradigm. The token paradigm described in Chapter II is convenient and could be transferred from one species to the other, especially in species habituated to manipulate objects with their beak. Cockatiels did not use their beak as much as other parrots species do, and they were shyer with humans than African grey parrots. A task could be designed in which birds only had to touch an object with their beak to receive the appropriate rewards and with no need to put the selected object in the experimenter's hand. Since the colony of cockatiels was created only a few months before the food-sharing experiment, which was the first experience ever done with these birds, I thought it would be too much work to train birds for the PCT task. The aviary was also not very suitable to put a table and to interact with cockatiels the same way we did with parrots. Now, since the birds are in the laboratory for few years, we can probably try to habituate them to this paradigm.

2) Defining the emotional link between mates

I am especially interested by the quality of the bond shared by mates in birds. The initial project of this thesis was to compare cooperative abilities of familiar birds and mates. I also wanted to study if Theory Of Mind and Empathy would enhance such cooperative tendencies. It is likely that long-term monogamy is maintained over time for other valuable reasons than fitness and reproductive success. Indeed some birds are forming monogamous pair bonds for life (Black, 2001) which could be costly, especially for males which could only reproduce with one single partner (Freed, 1987). These monogamous birds are sometimes living their entire life together like in biennials albatrosses that meet the same partner for their entire life (Bried et al., 2003), spend time in proximity, shared many life experiences and affiliative

behaviors. The “grieving” of the goose who lost its livelong mate described by Konrad Lorenz (Lorenz, 1966), or even the consolation provided by bystander after a fight observed in rooks (Seed et al., 2007) and ravens (Fraser & Bugnyar, 2010a) can let us think that these preferred associations can be mediated by affiliation and its emotional underpinning. To my knowledge, no studies evaluated the emotional link between mates, and how this mutual particular relationship could influence behavioral compatibility, reproductive success but also enhance cooperation and prosociality.

I would also be especially interested to see the emergence of more studies investigating Theory Of Mind-like abilities between sexual partners. Indeed, it is very likely that long-term sexual partners are selected to recognize and identify the other’s needs and intentions in order to synchronize and cooperate more efficiently. The experiments involving desire state attributions and food sharing in European jays are promising (Ostojić et al., 2013, 2016) and it would be thrilling to see the emergence of more experiments testing the link between mates and its consequences in cooperation. Most of the cooperative actions involving PCT token exchanges or loose string tasks involved familiar individuals but the degree of affiliation between partners was not always assessed (Drea & Carter, 2009; Horner et al., 2011), which is a crucial information to predict success in a dyad.

6) **Conclusion**

Our results demonstrated the existence of prosociality in psittacids via both artificial experimental task and more natural settings like food-sharing. Nevertheless, we cannot conclude on the ability of individuals to understand the other’s needs and desire to receive a food reward. More tested individuals are needed to draw a general conclusion on prosociality in an artificial task with these birds. Our cockatiels probably shared food to create and strengthen bonds but also for reciprocity and interchange. Siblings shared food at the highest rate and also exchanged many affiliative behaviors. Affiliation, which is maintained by

natural selection, could be one of the main mechanism triggering prosociality. One thing we know for sure while observing our results is that quality of the bond between individuals play an important role. In our experience with the playback of distress calls, birds reacted more to the calls of partners with which they shared a strong affiliation and they could be siblings, mates or "friends" spending time in proximity and exchanging allopreening. Interestingly, in intimidating situations, jackdaws displayed the same tendency and seemed to preferentially spend time with their sexual partners. This last experiment did not test prosociality or even empathy but it gave us some insights on birds' behavioral responses when confronted to a stressful situation with a preferred or a non-preferred partner. Once again, the quality of the bond seems to have an importance here. However, many studies still need to be done, and many data in psittacids and corvids are required to better understand the complexity of social life in these birds. Even if they share a strong bond with their sexual partners, other studies demonstrated that birds usually share crucial bonds with siblings (Stamps et al., 1990; Wanker, 1999) but also with other affiliates, of different sex (Boucherie et al., 2016). We also need to determine new methods to quantify emotions to better understand the implication of empathy as a potential driver of prosociality. Upcoming cross-species studies on "feathered apes" fascinating social organizations and cognitive abilities will give us for sure new insights to better understand their world.

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Appendices

Appendix I

Unpublished results and observations

Affiliation and dominance over a three years period in cockatiels

Two different types of observation have been conducted with cockatiels to assess the global social structure of the group: Affiliation and dominance.

1) Affiliation

First, I did "affiliation observations" sessions, with *ad libitum* observation of both aggressive behaviors and socio-positive exchanges. Each test was 20 minutes long, and all birds' behaviors were recorded at the same time in the aviary with a camera.

Five sessions of affiliation observations were performed: the first one in April 2014 (110 minutes of observation), the second one in January 2015 (420minutes of observation), the third one in April 2015 (360 minutes of observation), the fourth one in October 2015 (340 minutes) and the last one in June 2016 (320 minutes of observation).The three variables analyzed were: the frequency of allopreening, the frequency of solicitation of allopreening and the time spent in proximity (in seconds). See below pictures illustrating each behavior.

Figure 1. General view of the aviary during affiliation observations

Figure 2. Examples of solicitation of allopreening recorded during affiliation observation sessions: (a) between two males Rama and Bahloo (b) between two females Callisto and Sita and (c) between one male and one female Nephtys and Bahloo.

Figure 3. Example of allopreening

Figure 4 Two birds are in proximity when they can touch each other without moving their feet. (a) Nephtys and Seth in proximity (b) Bahloo, Nephtys and Seth in proximity. In this latter case, Bahloo (on the left) and Nephtys (in the middle) are in proximity and Nephtys and Seth (on the right) are in proximity but Bahloo and Seth are too far away from each other to be in proximity.

2) Dominance

A second test was conducted to assess dominance relationships in a food competition experimental paradigm. After a food-deprivation of approximatively 2 hours, a cup filled with millet was put in the aviary on the table on a half circle of kraft paper defining the zone of approach (diameter: 30 cm). The zone of approach was defined has a half-circle, positioned in front of the table edge in order to obtain a better filming view and see all the birds eating at the same time. Each test was videotaped until the cup was totally emptied by the bird (approximatively 4 minutes). All individuals were free to approach and eat. The test began when the cup was filled with millet.

Four sessions of dominance tests have been conducted in three years: one in May 2014 (7 tests), one in February 2015 (14 tests), one in July 2015 (11 tests) and a last one in June 2016 (12 tests).

The variables kept for analysis were the order of arrival, the latency before entering the zone of approach (in seconds), the frequency to eat, the time spent eating and the number of agonistic interactions won per bird.

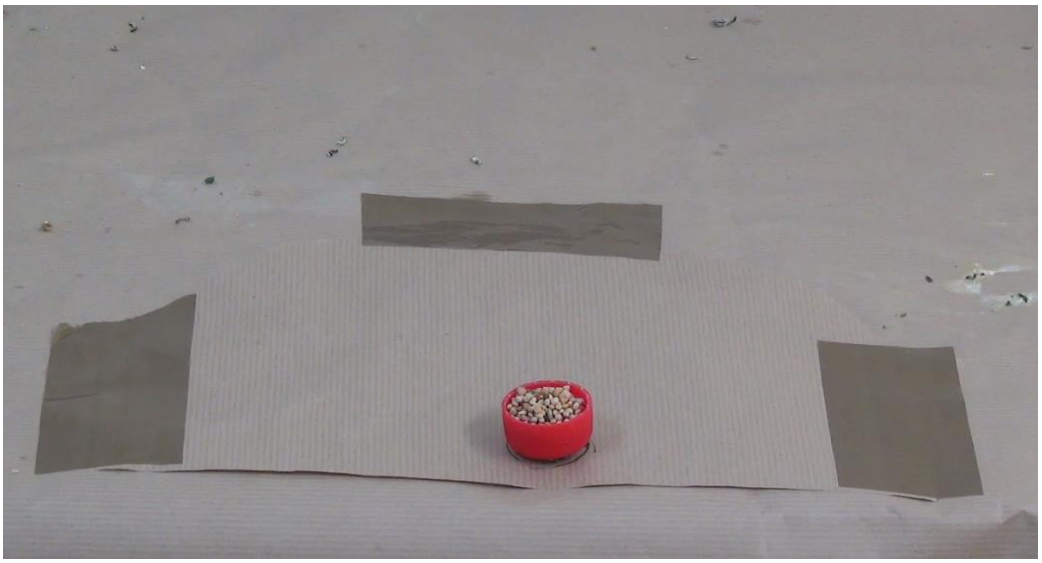

Figure 5. Experimental set-up. The cup filled with millet was put in the middle of the zone of approach (diameter: 30 cm).

Figure 6. Birds during a session of dominance task.

Prosocial Choice Task (PCT) in cockatiels and jackdaws

I wanted to replicate the prosocial experiment conducted by (Schwab, Swoboda, Kotrschal, & Bugnyar, 2012). Two birds, one actor and one receiver were tested in a PCT experiment in which birds had to open Plexiglas boxes containing reward either for themselves, for their partners or for both participants. Boxes could be opened via sliding lids which could be only pulled from the actor's side with a string. Each box was separated in two compartments with the actor side on the left and the recipient side on the right. Birds were separated from their partner by a grid. The actor had the possibility to open one of the two boxes and the receiver could not open any boxes. Two conditions were investigated: (a) prosocial condition in which the bird could either choose to open the box with only one reward for itself or the box in which both the actor and the receiver obtained a reward (b) altruistic condition in which the bird could only give a reward to its partner and did not receive any reward for itself.

The aim with jackdaws and cockatiels was to test two different types of dyads for each test: birds would have been tested either with a preferred partner (siblings, friends or sexual partner for cockatiels and mates for jackdaws) or a non-preferred familiar partner.

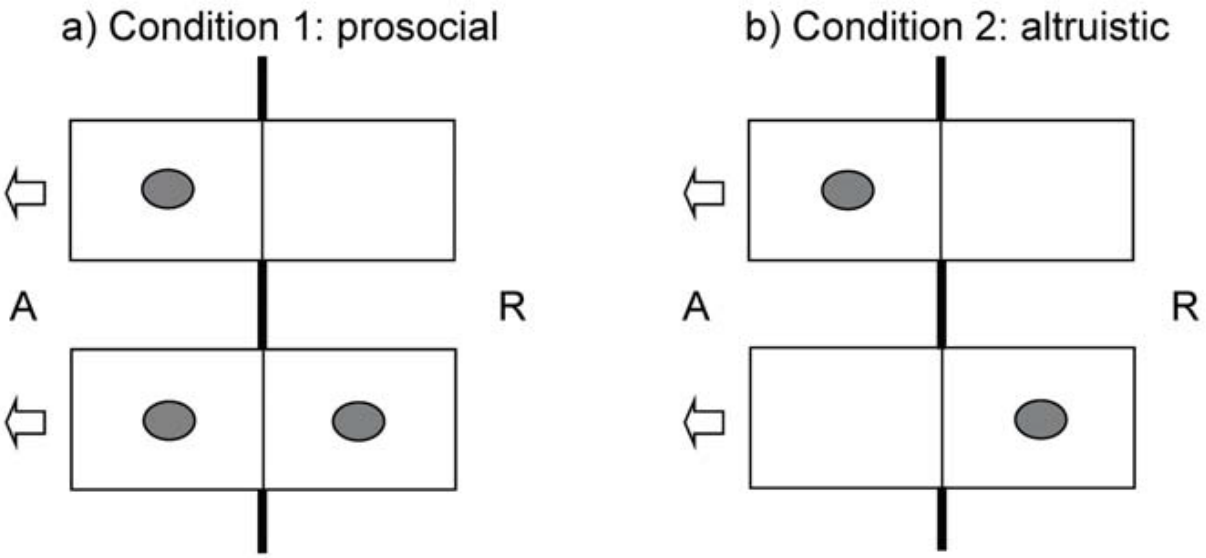

Figure 7. Experimental set-up (from Schwab et al., 2012

a) Jackdaws

Six mated pairs of jackdaws (*Corvus monedula*) were tested from February to April 2016 with one bird always acting as the donor and one bird always acting as the receiver. Birds quickly understood how to open boxes while using strings. Birds were trained with the control condition: one box was filled on both sides with halves worms and the second box was empty. Only the actor could pull the string and open the box. Only one string was provided to open the two boxes to prevent the actor to open the two boxes consecutively. The position of the two boxes was randomized across testing.

Actor	**Receiver**
Pronto (F)	Collins (M)
Cherokee (F)	Apache (F)
Tschock (M)	Jacomo (F)
Chimney (M)	Udo (F)
Tassilo (M)	Hedwig (F)

Table 1 Subjects tested in the PCT. (F) is for females and (M) for males

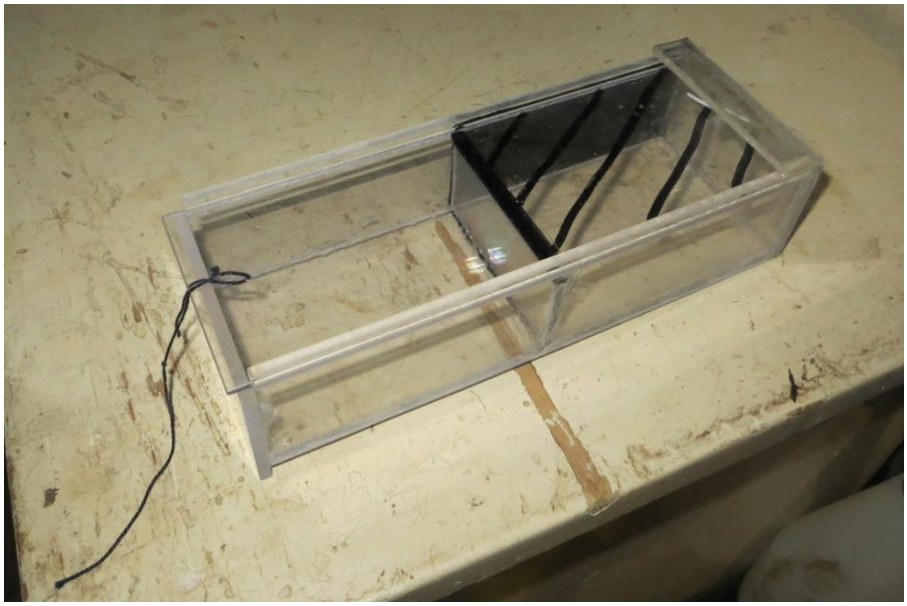

Figure 8. One of the two experimental boxes with its sliding lid attached to a string. Some black lines had been added since jackdaws, as many corvids, have some issue at working with translucent objects.

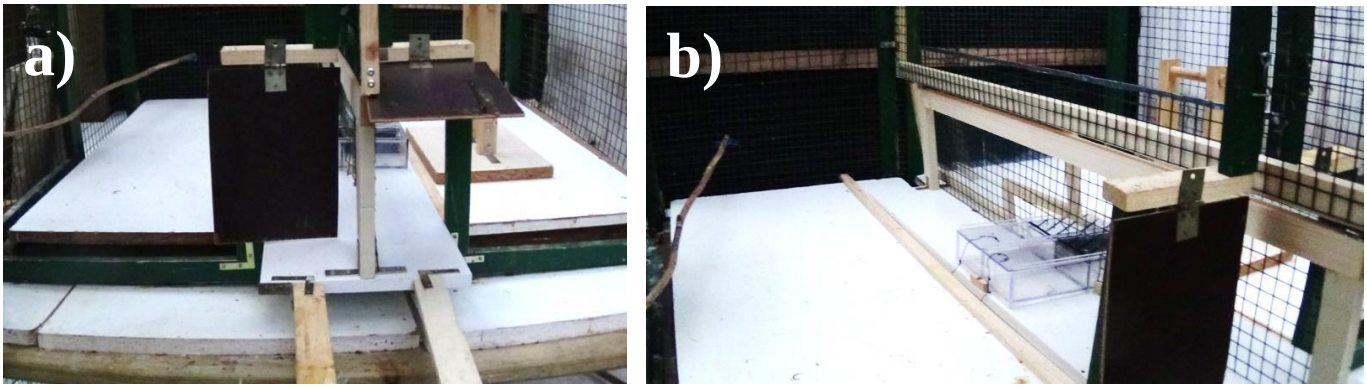

Figure 9. Experimental set up. (a) front view (b) inside the cage, view from the actor's side. The cage was separated in two compartments: the actor compartment on the left and the receiver one on the right. They were separated by a grid. The two boxes were put on a sliding tray which was inserted in the cage for each test. One single string was attached to the two sliding lids from the two boxes. Consequently the actor could only open one

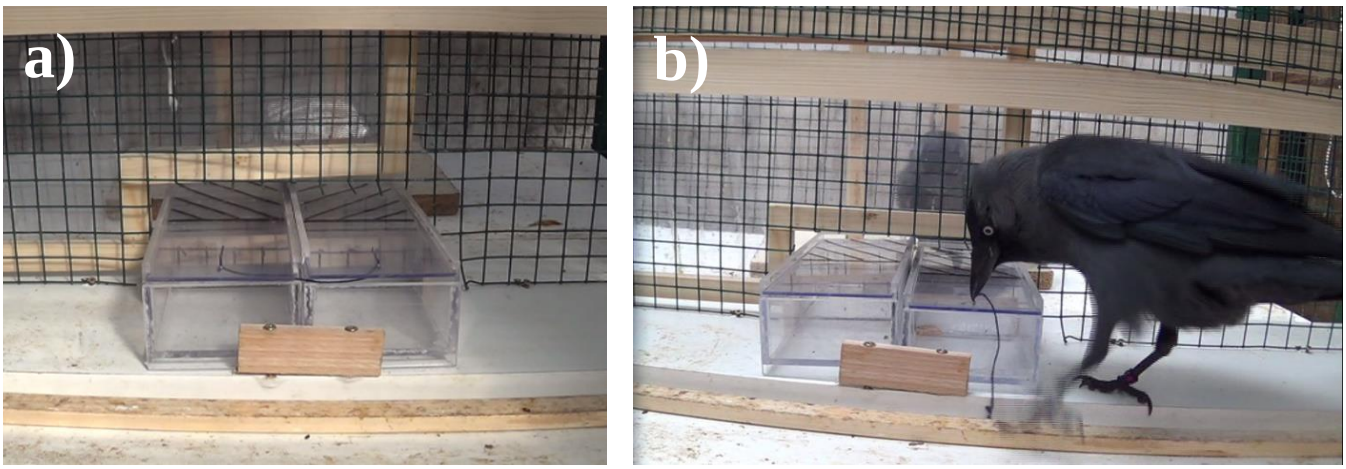

Figure 10. Birds in the experimental apparatus: (a) the actor is about to open the box. We can see the single string attached to the two lids. (b) the actor is pulling on the string to slide the box open. The receiver is waiting on the other side to eat a food reward.

Birds received two to three testing sessions per day with approximatively 10 trials per session per actor from the 8th March to the 16th of April 2016. In total, 2635 trials have been done. During each trial, the bird had the possibility to open one box. The criterion of success to pursue in step 2 was 9/12 openings of the box filled with foods on two consecutive days. An opening was considered as successful if the bird ate the reward. The boxes were removed and put out of reach from the actor with a system of sliding tray. Contrary to the jackdaws in Schwab experiment, which were able to choose the baited box in 2 to 3 days of habituation,

our jackdaws continued to open boxes at random and did not seem to pay attention to the rewards inside the box. Unfortunately, only one female, Pronto, reached the criterion of success and opened the baited box significantly more than the empty box but she needed 250 trials to reach the success criterion. Other birds opened boxes randomly and could never been tested even though birds received 2635 trials. Three donors (Cherokee, Tschok and Choctaw) received 640 to 680 trials individually while Tassilo received 258 trials and Chimney only 141 since he was shyer.

At the end of April, the breeding season began and tests were stopped because the birds could not be tested anymore. Since only one bird reached the criterion of success, the experiment was also stopped at that time.

b) Cockatiels

The same experimental set-up has been constructed and adapted to cockatiels in Nanterre. Birds have been habituated to touch the string and open the lid via 11 sessions of 20 minutes, both in their housing aviary and in the experimental room. The experiment was conducted by a master student when I was than testing jackdaws in Bavaria (March-April 2016). Unfortunately no other data are available about habituation process and success with these birds. Cockatiels, which are highly neophobic birds were afraid by the experimental cage, but it is very likely that they could get habituated to it with more familiarization sessions.

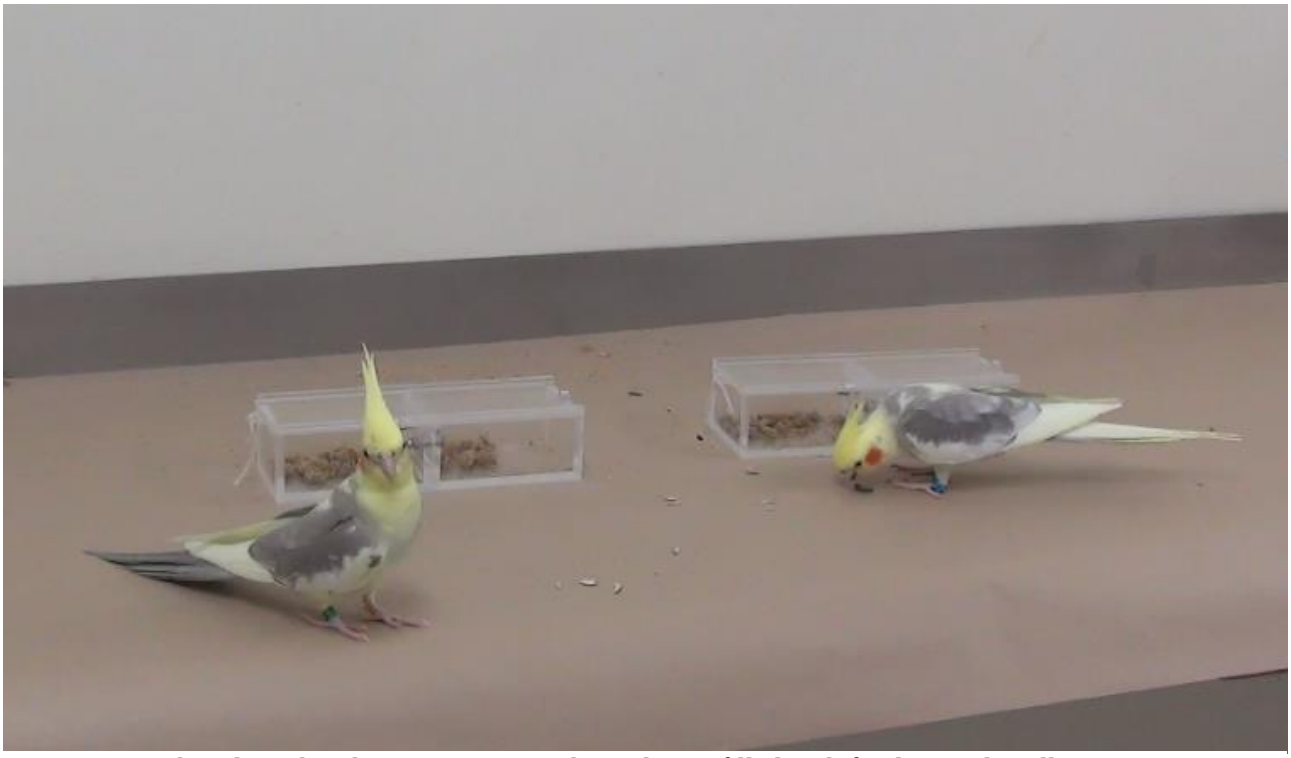

Figure 11. Cockatiels in their housing aviary with two boxes filled with food reward. Millet was put on string to motivate birds to open the boxes

Figure 12. Experimental cage. The two boxes were placed in the middle, the actor on the left, the receiver on the right.

Rescue behavior in cockatiels

To test empathy in cockatiels I wanted to adapt the protocol used by (Ben-Ami Bartal, Decety, & Mason, 2011), in which rats were trapped in a restrainer. Individuals were trained to open these restrainers and they were confronted to empty restrainers, trapped conspecifics or restrainers filled with objects or food rewards depending on the conditions. Even if the results of these experiments are still highly debated, they investigated experimental help and rescue, which are part of the empathy process. I wanted to test subjects' ability to help different partners, depending on the relationships shared with the trapped individual: preferred partners (siblings, mates, affiliated birds) or familiar non-partners that did not share high affiliation indexes with the subject. I hypothesized that subjects would be quicker to release partners than non-partners.

I designed new Plexiglas boxes adapted to cockatiels. Birds needed to pull on a metallic ring to open doors. Birds were trained to open the box with millet put on the ring with tape during a very first phase of habituation. Birds have been familiarized with the box either in their housing aviary or in the experimental room. They did 34 sessions of 20 minutes of familiarization in their housing aviary, with all other birds in September and October 2015. They also received 7 sessions of 20 minutes of familiarization in May 2016 in the experimental room. Birds were neophobic and seemed afraid by the box, at first. They were keener to open it and to explore it when they were tested in group in their housing aviary. Nevertheless, it was not possible to do the real test in the housing aviary since only two birds must be tested at a time. Consequently training sessions took place in the experimental room, but birds were shyer because they were less habituated to this room.

At the end of the seven sessions of habituation executed in May in the experimental room, 9 birds opened the box at least once. Nephtys, Merlin and Seth did open the box three times. Unfortunately, the experiment stopped at this moment.

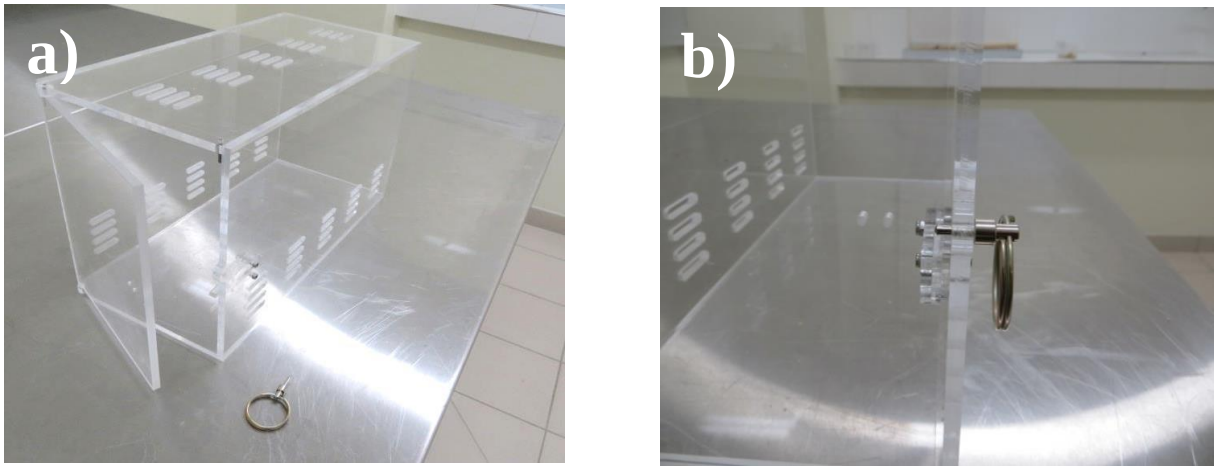

Figure 13. (a) Experimental box with its door opened and the metallic ring (opening mechanism) on the table (b) detail of the ring and of the opening mechanism of the door. The cockatiel had to pull on the ring to open the door

Figure 14. Habituation to rescue boxes in the experimental room. Bahloo and Seth, on the right, were pulling on the ring to eat the seed of millet stuck on it with tape. Nephtys, on the left, did not seem interested.

Habituation to mirror in cockatiels

Only a few species of birds have been tested with the mirror mark test in order to assess their ability to recognize their own image. Studies demonstrated that the ability to do the distinction between the self and the other, tested via the ability of self-recognition in a mirror could be mandatory to be empathic and to help others (Bischof-Köhler 1991, 2012). Magpies did positively respond to the mirror task (Prior et al., 2008) but the test has never been successfully replicated since, even if several birds species have been tested like jackdaws (Soler et al., 2014), New-caledonian crows *Corvus moneduloides* (Medina et al., 2011), jungle crows *Corvus macrorhynchos* (Kusayama et al., 2000) or African grey parrots (Pepperberg, Garcia, Jackson, & Marconi, 1995). The mirror test is a highly debated test but I always wanted to investigate it with cockatiels. I heard many anecdotes of researchers working with parrots and corvids who tried to do it and obtained no results, because, most of the time, the birds were not interested in it. Unfortunately these negative results have never been published. Since cockatiels possess a unique crest of feathers they could use it as a signal to communicate emotional states to others. I was thinking that a mark on this crest could be noticed and would attract the interest of the bird. I was thinking about using laser light or face powder to mark birds. Unfortunately, I lacked time to properly design a way to test birds and since cockatiels were very stressed when moved to the experimental room, I quickly decided to stop the experiment.

I familiarized birds in May 2015, while putting them in dyads in the experimental room with the mirror during 30 minutes. I formed dyads with affiliated animals to reduce their fear of novelty in front of the mirror. Millet was put in front of the mirror to motivate bird to come close to the object. Birds' behaviors were recorded with a camera, in front of the mirror and from a webcam put on top of the mirror. Seven birds participated to 2 sessions of 30 minutes of habituation. Three birds received only one habituation and one bird was too shy to be

moved in the experimental room and could not be tested at all (Sita). One bird (Merlin) sang and performed a courtship display during the first exposure to the mirror when tested with its sibling Bahloo. Bahloo ate in front of the mirror and did not show any sign of fear or interest. Some birds like Nephtys and Viviane accepted to stand close to the mirror but they did not move at all and seemed afraid. The other birds were very stressed when moved to the other room and they usually refused to stand on the table near the mirror or just froze on the table and did not move at all.

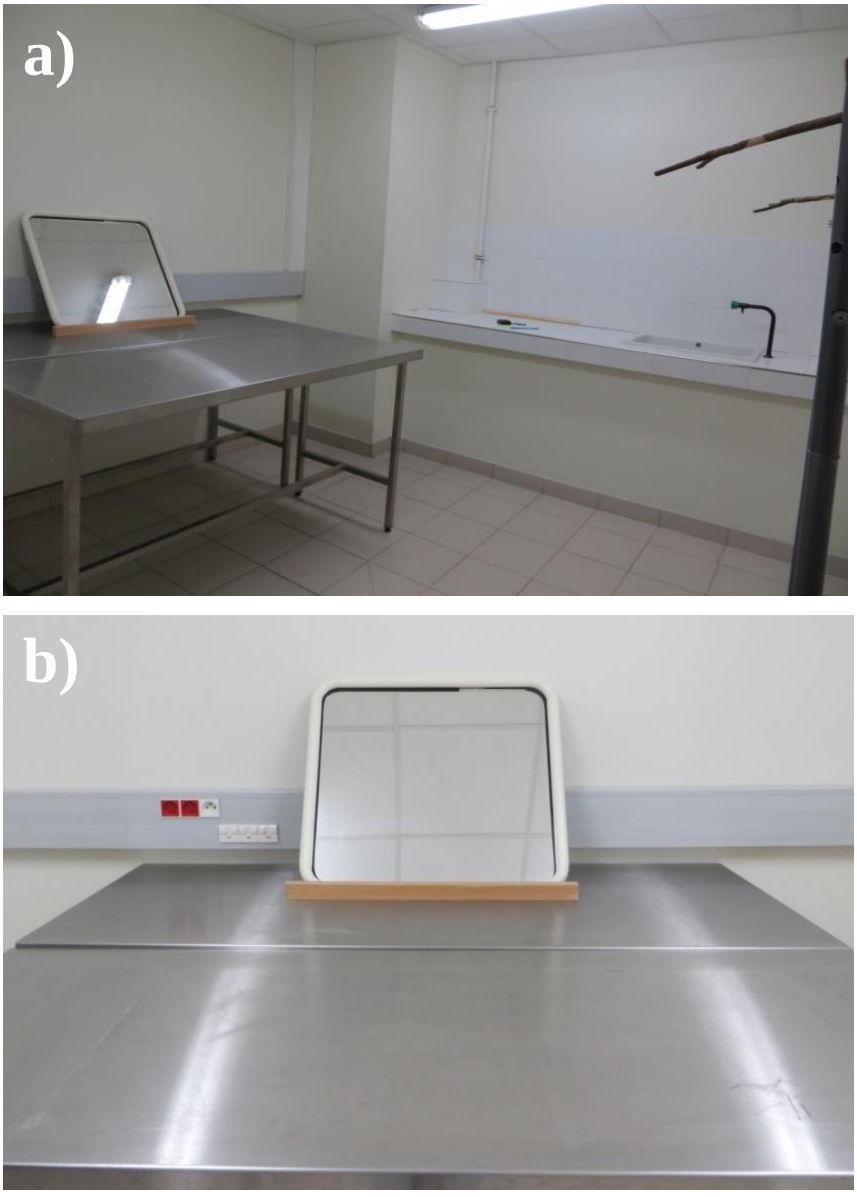

Figure 15. (a) Experimental set-up with the mirror in the experimental room (b) front view of the experimental set-up. Two stainless tables were put near the wall and a mirror was put near the wall also, so the birds could see them entirely in the mirror. Millet was put on the table and in front of the mirror

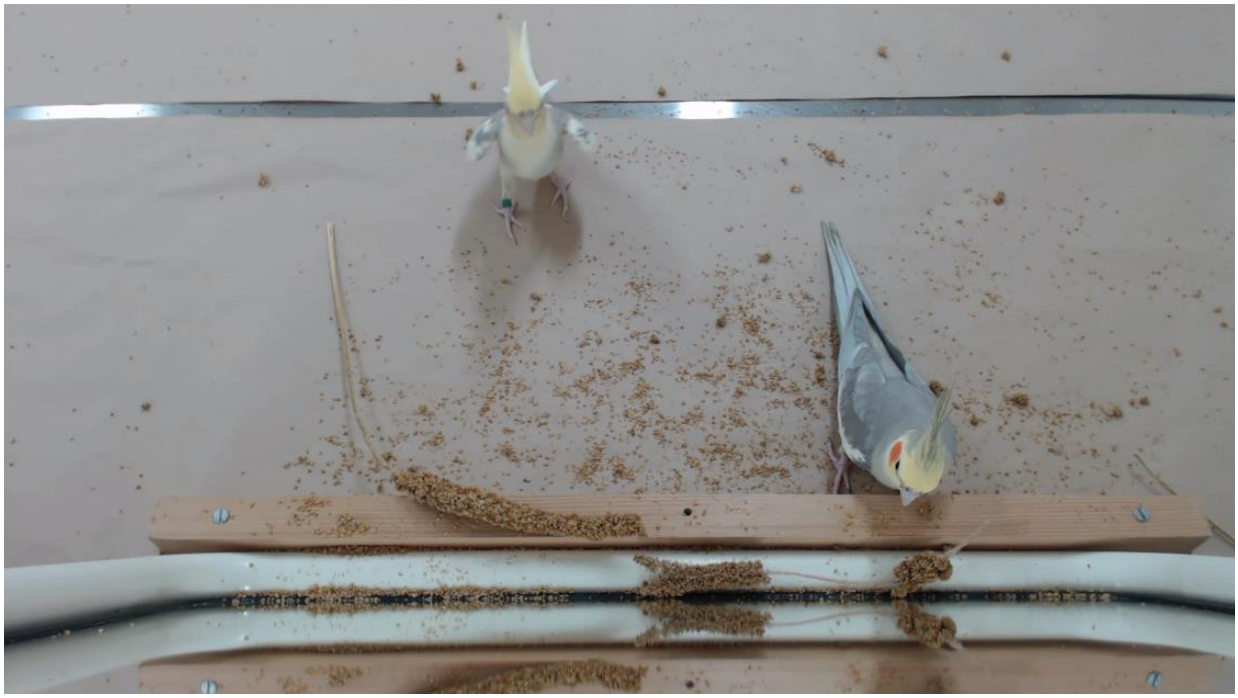

Figure 16. Merlin (on the left) ran, sang and performed a courtship display in front of the mirror while its siblings Bahloo ate millet in front of it. Courtship display is easily recognized by the shape of heart of the bird's wings (Webcam view from the top of the mirror)

Figure 17. Viviane (on the left) and Loki in front of the mirror (camera view in front of the mirror)

Dominance in jackdaws

A paradigm of food dominance was adapted to jackdaws to test the dominance in each group of bird in a food competition context. At the beginning we put 20 worms in a cup but the session was very short and we did not have time to observe agonistic interactions. Shy birds also had no chance to participate since all food was quickly eaten by boldest birds. We then changed the paradigm and observed birds' behaviors in the morning when we gave them a portion of food for the morning/or afternoon (birds were fed twice a day). The bowl was put on the floor. A square was drawn on the floor around the food bowl with a piece of chalk to materialize the zone of approach around the food bowl.

The experiment began when the cup was filled. The experimenter stayed in the aviary during the test and behaviors were recorded on camera. The test was over when birds stopped to come. Usually, test sessions were 20 minutes long. Twenty three sessions were realized: 11 for the first aviary and 12 for the second aviary. All birds were free to come during each experiment. Thirteen birds were present in aviary 1 (8 females, 5 males) and eleven in aviary 2 (6 females and 5 males).

During the video analysis, we collected the order of arrival for each bird, the latency before approach, the time spent eating, the number of times a bird could access food and the agonistic behaviors. The videos have been only partially analyzed at the moment.

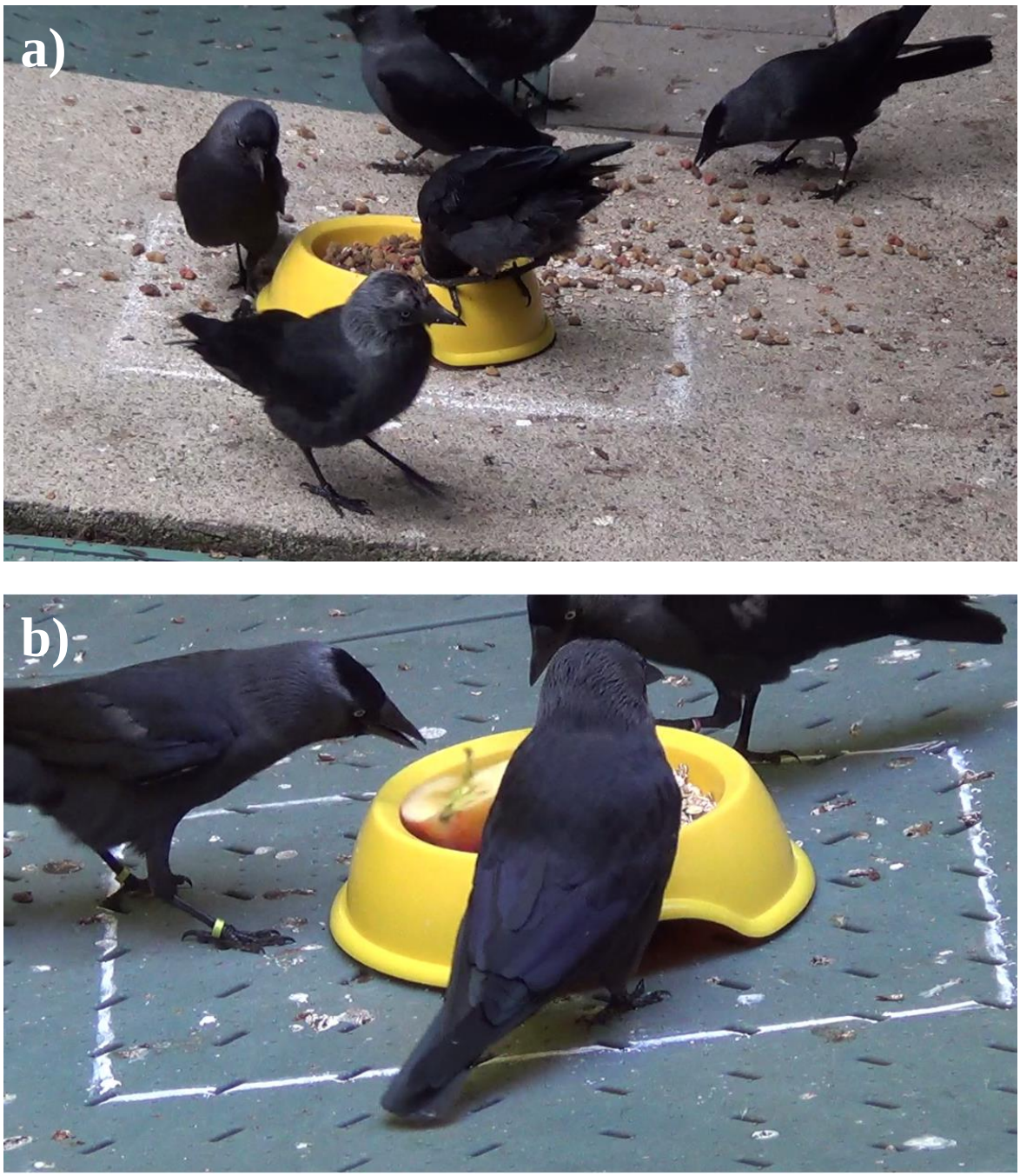

Figure 18. Dominance task set-up in (a) aviary 1 and (b) aviary 2. The bowl was filled every morning with the same amount of food in the same bowl: wet cat food, half an apple and muesli. A square was drawn on the floor (50 cm in diagonal) to represent the zone of approach.

Appendix II

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Appendix III

Curriculum vitae

Agatha **LIÉVIN-BAZIN**

PhD student in Ethology

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agatha.lievin@gmail.com

Nanterre, France

11.11.1988, Reims (51)

Permis B

RESEARCH EXPERIENCES

2013-2017 (4 years)

PhD student in ethology

Prosociality, social cognition and empathy in parrots and corvids

Laboratoire Éthologie Cognition Développement, Nanterre, France
Max Planck Institute for Ornithology, Seewisen, Germany

2012-2013 (9 months)

Research internship

Prosociality in capybaras and budgerigars

Laboratoire Éthologie Cognition Développement, Nanterre, France
Muséum National d'Histoire Naturelle (MNHN), Paris, France

2011 (3 months)

Research internship

Cooperation and tool use in jackdaws and New-Caledonian crows

Max Planck Intitute for Ornithology, Seewisen, Germany
Zoology group, Oxford, United Kingdom

2011 (5 months)

Research internship

Cognitive and motor deficits due to aging in grey-mouse lemurs

Laboratoire d'écologie générale, MNHN, CNRS, Brunoy, France

2010 (1 month)

Research internship

Manipulation, feeding and care of injured wild animals

CEDAF, Veterinary school of Maisons-Alfort, France

2010 (2 months)

Research internship

Cooperation and prosociality in african grey parrots

Laboratoire Éthologie Cognition Développement, Nanterre, France

---

2009 (1 month)

Research internship

Study of an european wolf pack during the youngs rearing period

Parc animalier de Sainte Croix, Rhodes, France

FORMATION

2012-2013 — **Master degree in Psychology (suma cum laude)**
Université Paris Ouest Nanterre la Défense, France

2009-2011 — **Master degree in Ethology (cum laude)**
Université Paris XIII-Villetaneuse, Sorbonne Paris Cité, France

2006-2009 — **Bachelor of Science in Biology (cum laude)**
Speciality: Cellular biology and physiology
Université Reims-Champagne Ardennes, France

LANGUAGES

English — **C1 level**
Test Toefl ibt: 106/120 in 2013

German — **B1 level**
Test onDaf in 2013

SOFTWARES

Animal behavior — Solomon coder® - Avisoft® -Sound Analysis Pro ®
Statistical analysis — R - StatXact® - SigmaPlot®
Design — Photoshop® - Indesign®

GRANTS

Mobility Grant (DIM Région Ile de France): 4000 euros for 3 years (2013-2016)

Additional Grant to PhD funding (DIM Région Ile de France): 5000 euros for 3 years (2013-2016)

« Humanités » Grant (L'humain impensé program): 3400 euros

MEMBERSHIP

Since 2011 — Société Française du Comportement Animal (SFECA)

Since 2015 — Association for the Study of Animal Behavior (ASAB)

HOBBIES

Outreach
Member of the **Café des Sciences** association since 2017
http://www.cafe-sciences.org/
Creation of the website « ***Le nid de pie »*** in 2016 *(http://leniddepie.com)*

Presentator of 6 conferences on zoology during online events on youtube (**Geek Faëries**, **Headbang**) since 2014
https://www.youtube.com/channel/UCfsKk7Rd5wEkGMPdZvqvHmA

Drawing
Illustrator in the ***Mutatis mutandis*** collective since 2013
Illustrator and secretary of the ***Obscurus Presse*** association since 2009

Travels — Several travels in Europe, Africa, North America, Asia and Australia

PUBLICATIONS

Papers

Liévin-Bazin A, Pineaux M, Daubord L, Rohée M, Gahr M, Bovet D, von Bayern AMP. Effect of social relationships on novel object exploration by neophobic jackdaws (*Corvus monedula*). Submitted to *Ethology*

Liévin-Bazin A, Bovet D, Pineaux M, Le Covec M, Gahr M, von Bayern AMP. Food-sharing and affiliation: an experimental and longitudinal study in cockatiels (*Nymphicus hollandicus*). Submitted to *Animal Behaviour*

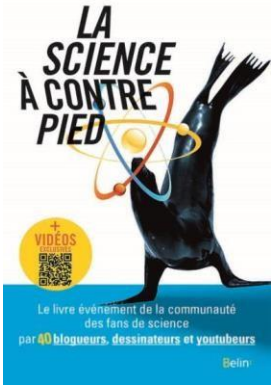
Liévin-Bazin A, Pineaux M, Clerc O, Gahr M, von Bayern AMP, Bovet D. Emotional responses to conspecific distress calls are modulated by affiliation in cockatiels (*Nymphicus hollandicus*). Under revision at *PlosOne*

Liévin-Bazin A, Péron F, Rat-Fischer L, Colléony A, Nagle L. & Bovet D. Do parrots act prosocial ? Under revision at *Behavioral Proccesses*.

Lalot M, **Liévin-Bazin A**, Bourgeois A, Saint Jalme M, Bovet D. Prosocial and selfish strategies in capybaras (*Hydrochoerus hydrochaeris*) in a non-reproductive context. Submitted to *Behavioral Processes*

Languille S, **Liévin-Bazin A**, Picq J-L, Louis C, Dix S, De Barry J, Blin O, Richardson J, Bordet R, Schenker E, Djelti F, Aujard F. 2014. Decline of psychomotot and mnesic functions across aging in mouse lemur primates. *Frontiers in Behavioral Neuroscience*. 8:446. doi: 10.3389/fnbeh.2014.00446

Book chapters



Liévin-Bazin A. Les oiseaux aussi en ont dans le ciboulot. Text and illustrations. In *La science à contrepied*, Editions Belin, 2017.

Liévin-Bazin A, Debove D, Yassine L, Les écureuils sont des tueurs d'enfants et autres désillusions sanglantes. In *La science à contrepied*, Editions Belin, 2017. Text and illustrations.
Vidéo: https://www.youtube.com/watch?v=YIxmBOAcWVk

Oral Presentations (8 as speaker, 5 at an international conference)

Liévin-Bazin, A., Pineaux M., Bovet D. & von Bayern AMP. I share because I care ? A longitudinal study of food sharing in cockatiels (Nymphicus hollandicus), 35th International Ethological Conference (IEC), Estoril, Portugal, 30th of July-4th of August 2017

Liévin-Bazin, A., Pineaux M., Bovet D. & von Bayern AMP. Affinity, food sharing and emotional contagion in cockatiels and jackdaws. **Invited speaker in Kevin Laland's lab**, St Andrews, United Kingdom, 21rd of april 2016

Liévin-Bazin, A., Le Covec M., Pineaux M., Bovet D. & von Bayern AMP. The role of food-sharing: a comparative study in cockatiels and jackdaws. Workshop "animal communication" Franco-German Symposium, Nanterre, France . 10-11th of Decembrer 2015

Liévin-Bazin, A., Bovet D. & von Bayern AMP "Je sais ce que tu ressens": L'empathie et la prise en compte de l'autre chez l'animal. Journée d'études Anthropologie, éthologie: lectures transversales (projet Humanités "l'humain impensé"), Nanterre, France, 6th of November 2015

Liévin-Bazin, A, Bovet D. & von Bayern AMP "I know how you feel": Mesurer différents degrés d'empathie chez les animaux. Séminaire: réflexions sur des rencontres entre des animaux et des humains: médiations, parc de loisirs, laboratoire...(projet Humanités "l'humain impensé"), Nanterre, France, 2nd of November 2015

Liévin-Bazin A., Clerc O., Ung D., von Bayern AMP & Bovet D. Emotional contagion in response to distress calls in cockatiels. 34th International Ethological Conference. Behavior (IEC), Cairns, Australia, 9-14th of August 2015

Liévin-Bazin A, Clerc O, Bovet D. & von Bayern AMP. Emotional contagion in cockatiels. Annual meeting of the French Society for the Study of Animal Behavior (SFECA), Strasbourg, France, 21-23rd of April 2015

Liévin-Bazin A, Bovet D. & von Bayern AMP. Theory of mind and empathy in psittacids and corvids. International Workshop - Franco-German Symposium. Max Planck Institute for Ornithology, Seewisen, Germany, 15th of December 2014

Lalot M, **Liévin-Bazin A**, Bonnaffe W, Bloch C, Barhoumi C. & Bovet D. Prosocial behaviours in Mammals. International Workshop-Franco-German Symposium. Interactions, communications and learning: from invertebrates to humans. La Défense, France, 2-4th of October 2013

Lalot M, Prager N, Schaffner P, **Liévin-Bazin A**. & Bovet D. Prosociality in mammals & birds: a difference between genders ? Franco-German Symposium, Seewiesen, Germany, 3rd of December 2012

Colléony A, Lalot M, **Liévin-Bazin A**, Dollion N, Malassis R, Péron F. & Bovet D. Are African grey parrots (Psittacus erithacus) prosocial ? 7th Ecology & Behaviour Meeting, SERL 2011, Rennes, France. 2-6th of May 2011

Péron F, Colleony A, **Liévin-Bazin A**, Malassis R, Dolion N, Nagle L. & Bovet D. Behavioural organisation and social modulation of cooperative actions in budgerigars. Student Forum on Cooperation Research, Londres, United Kingdom, 9th of December 2010

Posters (10 as 1st author, 4 presented at international conferences)

Liévin-Bazin A, Pineaux, M., Bovet, D. & von Bayern AMP. Partage alimentaire chez les perruches calopsittes et liens avec l'affinité. Journées de la recherche, Université Nanterre, France, 27-28th of April 2017

Liévin-Bazin A. Social networks in jackdaws and cockatiels. Social Network Analysis workshop, Max-planck Institute for Ornithology, Contanz University, Germany, 17-19th of January 2017.

Liévin-Bazin A, Pineaux, M., Bovet, D. & von Bayern AMP. Food sharing and affinity: a longitudinal and comparative study in cockatiels and jackdaws. 8th European Conference on Behavioural Biology (ECBB)**.** Vienna, Austria, 12-15th of july 2016

Liévin-Bazin A, Le Covec M., Bovet, D. & von Bayern AMP. Partage alimentaire chez les perruches calopsittes (Nymphicus hollandicus). Journée de la Recherche, Université Nanterre, France, 9th of Décember 2015

Liévin-Bazin A, Le Covec M., Bovet, D. & von Bayern AMP. Food sharing in cockatiels (Nymphicus hollandicus). GDR d'éthologie et journée IFE, Villetaneuse, France, 12-14th of October 2015

Liévin-Bazin A, Ung D, Dubedat M, Bovet D. & von Bayern AMP. Food-sharing as predictors of social bond origins and affinity in a group of young cockatiels. Journées de la recherche, Université Nanterre, France, 14th of November 2014

Liévin-Bazin A, Ung D, Dubedat M, Bovet D. & von Bayern AMP. Food-sharing and social bonds origin in young cockatiels (Nymphicus hollandicus). 7th European Conference on Behavioural Biology (ECBB). Prague, Czèch republic, 17-20th of July 2014

Liévin-Bazin A, Ung D, Dubedat M., Bovet & von Bayern AMP. Partage alimentaire et origine des liens sociaux chez de jeunes perruches calopsittes. Annual meeting of the French Society for the Study of Animal Behavior (SFECA), Nanterre, France, 8-10th of July 2014

Liévin-Bazin A, Ung D. & Bovet D. Numerical cognition in female canaries (Serinus canaria). Annual meeting of the French Society for the Study of Animal Behavior (SFECA), Dijon, France, 19-21st of November 2013

Lalot M, **Liévin-Bazin A**, Caré S, Sagne S, Bocquet C. & Bovet D. Prosocial behaviours in mammals. Annual meeting of the French Society for the Study of Animal Behavior (SFECA), Dijon, France, 19-21st of November 2013

Liévin-Bazin A, Serrÿn C, Feret A, Lalot M. & Bovet D. Prosociality in budgerigars and capybaras. 3rd CompCog conference, Vienna, Austria, 03-05th of July 2013

Languille S., **Liévin-Bazin A**., Picq J.-L., Louis C., Dix S., De Barry J., Auffret A., Richardson J., Schenker E., Lestage P., Aujard F. Behavioral profile across aging of a non-human primate, Microcebus murinus. Annual Meeting of Society For Neuroscience (SFN), New Orleans, USA, 13-17th of October 2012

Péron F, **Liévin-Bazin A**, Colleony A, Malassis R, Dollion N, Nagle L. & Bovet D. Testing cooperative abilities in budgerigars (Melopsittacus undulatus). INCORE consortium (Integrating Cooperation Research Across Europe). Cooperation: An Interdisciplinary Dialogue. Budapest, Hungary, 17-18th of September 2010

Péron F, Colleony A, **Liévin-Bazin A**, Malassis R, Dolion N, Nagle L. & Bovet D. Prosocial behaviour as a condition to maintain cooperation in a token exchange task in African grey parrots. INCORE consortium (Integrating Cooperation Research Across Europe). Cooperation: An Interdisciplinary Dialogue. Budapest, Hungary, 17-18th of September 2010.

OUTREACH

Conference

« Les piafs en ont aussi dans le ciboulot », présentation du livre « La science à Contrepied » avec les membres du Café des sciences, Librairie le Divan, Paris 15e , 9th of May 2017

« Crâne de piaf ? », 25èmes journées Nature « des bêtes pas si bêtes » organized by AVCA Avermes, Avermes, France, 26th of May 2016

Empathy in cockatiels. Apérosciences, National Museum of Natural History, Paris, France, 19th of February 2015

Presse article

Le Figaro: « Les corbeaux, as de la planification et du self-contrôle », 18th of July 2017
http://www.lefigaro.fr/sciences/2017/07/17/01008-20170717ARTFIG00204-les-corbeaux-as-de-la-planification-et-du-self-control.php

Santé magazine n°469 : « Développer son empathie ; les animaux aussi », 2nd of December 2014

le Journal du dimanche : « l'intelligence des corbeaux », 8th of June 2014
http://www.lejdd.fr/Societe/Sciences/L-intelligence-des-corbeaux-670668

Radio

La Méthode Scientifique, France Culture « Malin comme un corbeau », 11th of September 2017
https://www.franceculture.fr/emissions/la-methode-scientifique/malin-comme-un-corbeau

les aventuriers de l'inconnu, RTL « Cervelle d'oiseaux » 17th of July 2017
http://www.rtl.fr/actu/societe-faits-divers/cervelles-d-oiseaux-7789276726

les Savanturiers, France Inter « En direct du Salon du Livre de Paris » 26th of March 2017
*Book promotion for « La science à Contrepied »,*éditions Belin
https://www.franceinter.fr/emissions/les-savanturiers/les-savanturiers-26-mars-2017

Les matins d'été de France culture : « Malin comme un corbeau », 7th of July 2014
http://www.franceculture.fr/emission-les-matins-d-ete-1ere-partie-conference-sociale-yann-algan-et-patrick-fridenson-2eme-partie

Sur les docks, France culture : « L'intelligence des perroquets », 14th of April 2014
http://www.franceculture.fr/emission-sur-les-docks-%C2%AB-l%E2%80%99intelligence-du-perroquet-%C2%BB-2014-04-14

Podcast

Podcast Madmoizelle n°18 C'est tout ce qu'on aime *« Steven Universe et éthologie (étude du comportement animal) »* 15th of June 2017
https://www.youtube.com/watch?v=hhGqYj4G31Y

Podcast Science n°303 *« L'éthologie avec Agatha »,* 14th of June 2017
https://www.podcastscience.fm/dossiers/2017/06/25/ethologie/

Web

Animator of the collaborative twitter account « La bio au labo »,3rd-8th of April 2017,
https://storify.com/laBioauLabo/agatha

Television

Le monde de Jamy, France 3*: « Ces animaux si proches de nous* », 12th of April 2017
https://www.youtube.com/watch?v=JjBHcOxK2GA

E=M6, M6: « Aliments, corps, animaux: toutes les questions simples qu'on n'ose pas poser expliquées par la science ! », 12th of June 2016

E=M6, M6 : « Idées reçues sur l'alimentation, la santé, les animaux: E=M6 démêle le vrai du faux », 8th of November 2015

C dans l'air , France 5 : « Mon chat est-il une personne ? », 2nd of January 2015
https://www.youtube.com/watch?v=ymJoVwdYMrA

TEACHING

Teaching at Nanterre University

Biology and genetic courses, 88 hours, 1st year student in Psychology (Bachelor)

Practical courses of compared Psychobiology, 150 hours, 3rd year student in Psychology (Bachelor)

Biology courses « *Diversity of living creatures* », 36 hours, MSc students (1st year of MsC; future teachers; Master MEEF, SUFOM)

Biology courses, 46 hours, MSc students (2nd year of MsC, future teachers; Master MEEF, SUFOM)

Ethology course « *Tool use in animals* », 2 hours, Université de la Culture Permanente

Initiation to ethology course, 3 hours, MSc in anthropology, UFR Anthropologie-LESC

325 hours of teaching over 3 years

Supervision of students

4 students in Bachelor of Science or Psychology: Myriam Dubédat (Université Orsay, L2); Laëtitia Fontaine (voluntary internship Université Nanterre, L2); Morgan Rohée (voluntary internship Université de Rennes, L3), Maureen Konrad (Université Paris Descartes, L3)

8 students in Master of Ethology: Diana Quent (Université Paris Villetaneuse M2 pro); Olivier Clerc (Université St Etienne M1); Louise Grosboillot (Université de Franche-Comté L3 + Université Paris Villetaneuse M1); Mathilde Le Covec (Université Paris Villetaneuse, M1); Delphine Soulet (voluntary internship post M2 Université Paris Villetaneuse), Julia Mariette (Université Paris Villetaneuse voluntary internship post M1), Lucie Daubord (Université Paris Villetaneuse, voluntary internship post M1), Noémie Pinchaud (Université Paris Villetaneuse voluntary internship M2)

OTHERS

Fundation of the actual cockatiel colony of the lab: aviary fitting, creation of perches and accessories, interactions with bird breeders, selection of the individuals…with the help of Philippe Groué.

Design of apparatuses. Creation of four plexiglas boxes for two prosocial experiments, adapted to cockatiels'morphology with Jean-Pierre Boucher (JPB conseils & XY Production)

Member of the organizing comitee for the seminar: réflexions sur des rencontres entre des animaux et des humains: médiations, parc de loisirs, laboratoire...(projet Humanités "l'humain impensé"), Nanterre, France, 2nd of November 2015

Member of the organizing comitee for the SFECA 2014 conference
Management of the book selling activity (« livres DUNOD ») and creation of the event's logo

PhD students representative (2015-2017), Lab meeting advisor

Management of lab's website with Anne-Bobin Bègue's help

Abstracts

Zusammenfassung

Im Tierreich gibt es Arten mit komplexer Gruppenstruktur, in denen Individuen aufwendige soziale Beziehungen mit Artgenossen eingehen. Prosoziales Verhalten, ein Verhalten zum Wohle Anderer, tritt bevorzugt zwischen Individuen auf, die eine starke gegenseitige Bindung aufweisen. Prosozialität beruht auf Empathie-Fähigkeit, die wiederum ein gewisses Verständnis der emotionalen Lage von Artgenossen voraussetzt. Vögel, insbesondere Papageien und Krähen, sind geeignete Modelle, um Zusammenhänge zwischen sozialer Bindung und prosozialem Verhalten zu untersuchen: sie bilden Langzeit-monogame Paare, die das Jahr hindurch miteinander kooperieren. Ziel dieser Doktorarbeit ist es, herauszufinden, wie soziale Bindungen (verwandtschaftlicher, sexueller, oder freundschaftlicher Natur) prosoziales Verhalten und Empathie beeinflussen. Zu diesem Ziel wurden Studien über Futterteilen und Verhaltensreaktionen auf Stress in verschiedenen sozialen Kontexten durchgeführt. Nymphensittiche (*Nymphicus hollandicus*) reagierten stärker auf Warnrufe ihres Partners als auf die eines anderen Gruppenmitglieds. Ebenso teilten verwandte Sittiche häufiger Futter miteinander als mit anderen Individuen. Verschiedene Papageienarten bevorzugten in einer Entscheidungssituation prosoziale über egoistische Optionen, wobei unklar bleibt, ob sie die Perspektive ihres Partners verstanden. Dohlen (*Coloeus monedula*), die mit einem für sie unheimlichen neuen Objekt konfrontiert wurden, verbrachten mehr Zeit in gegenseitiger Nähe, wenn sie mit Ihrem Partner als mit einem anderen Individuum getestet wurden. Sie verhielten sich aber in Gegenwart ihres Partners nicht mutiger. Die Ergebnisse legen nahe, dass Bindungen zwischen Individuen prosoziales Verhalten und empathische Reaktionen aufeinander beeinflussen.

Schlüsselwörter: Prosozialität , Soziale Kognition, Empathie, Vögel, Krähen, Papageien

Résumé

Dans le règne animal, certaines espèces présentent une organisation en groupe complexe, permettant l'établissement d'interactions sociales plus ou moins élaborées entre les individus. Les comportements prosociaux, visant à améliorer le bien-être de l'autre, apparaissent préférentiellement entre animaux qui partagent une grande affinité ; ces comportements sont probablement favorisés par l'empathie, suggérant une prise en compte émotionnelle du partenaire. Les oiseaux, et particulièrement les corvidés et les psittacidés, se révèlent être d'excellents modèles pour étudier ce lien entre relation sociale et prise en compte de l'autre: ils forment des couples monogames sur le long terme au sein desquels une forte coopération existe. L'objectif de cette thèse est d'explorer comment le lien entre individus (familial, sexuel, amical) module les comportements prosociaux et empathiques. Les réactions des sujets sont évaluées via le partage de nourriture ou bien en observant une sensibilité accrue envers un congénère. Chez les perruches calopsittes (*Nymphicus hollandicus*), les oiseaux réagissent plus fortement au cri de détresse d'un oiseau préféré qu'au cri d'un autre congénère familier et les individus apparentés (frères et sœurs) partagent davantage la nourriture entre eux qu'avec les autres. Les perroquetsont tendance à être prosociaux mais la prise en compte de l'autre reste à confirmer. Les choucas des tours (*Coloeus monedula*), placés dans une situation nouvelle avec un autre oiseau, passent plus de temps à proximité de leur partenaire sexuel que d'un autre oiseau de sexe opposé. Ces différents résultats suggèrent qu'un lien d'affinité existe entre les individus et qu'il façonne leurs comportements en termes de prosocialité et d'empathie.

Mots clés : Prosocialité, cognition sociale, empathie, oiseaux, corvidés, psittacidés

Abstract

In the animal kingdom some species form complex social groups in which elaborated relationships between individuals occur. Prosocial behaviors, i.e. actions that benefit others, preferentially occur between closely affiliated individuals and may be driven by empathy, the ability to identify and share the emotional states of others. Birds, particularly corvids and parrots, are excellent candidates for investigating the link between social relationship and other-regarding behavior. They are long-lived and form long-term monogamous pair-bonds in which a high level of cooperation is seen throughout the year. The aim of this thesis is to study how the nature of a relationship (sibling, mate or friend) can modulate prosocial behavior and its underlying emotions in parrots and a corvid species. The approach was to study food-sharing or behavioral reactions to stressful situations such as distress call playback or exposure to novel objects, in different social contexts. Cockatiels (*Nymphicus hollandicus*) reacted more to the distress calls of a closely affiliated partner than to those of a non-partner, and they preferably shared food with affiliated, related individuals. Different species of parrots preferentially chose a prosocial option over a selfish one, but it remains unclear whether they took the other's perspective into account. Confronted with intimidating novel objects, jackdaws (*Coloeus monedula*) spent more time in mutual proximity when paired with their mate than when with a familiar opposite-sex non-partner. However, they were not bolder when accompanied by their mate compared to a non-partner. These results suggest that an emotional link exists between affiliated individuals and that this special bond drives their prosocial and empathic behavioral responses.

Key words: Prosociality, social cognition, empathy, birds, corvids, parrots